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PALEONTOLOGY

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VOLUME 34 MAY, 1960 NUMBER 3

CORDANIA AND OTHER TRILOBITES FROM THE LOWER AND MIDDLE DEVONIAN

H. B. WHITTINGTON

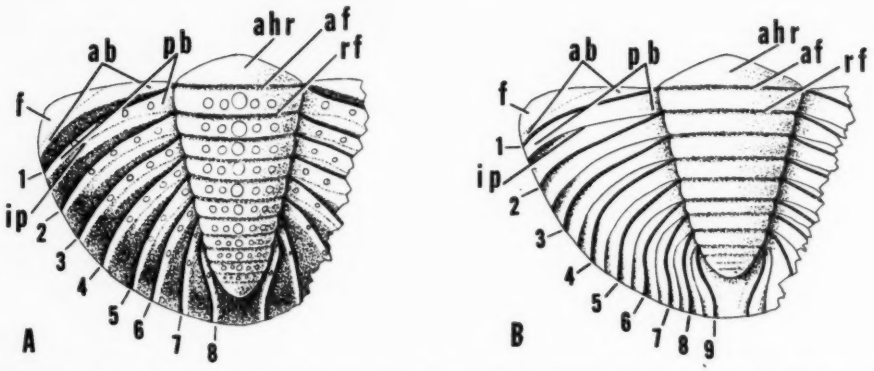
Museum of Comparative Zoology at Harvard College, Cambridge, Massachusetts

ABSTRACT—The type and five additional species of *Cordania*, from the Lower Devonian of Quebec, Maine, New York, Tennessee and Oklahoma, are described. Facial sutures are present, the anterior branches widely divergent; nine thoracic segments. *Mystrocephala* n. gen. (type species *C. pulchra* Cooper and Cloud) includes Lower and Middle Devonian species differing from *Cordania* in that cheek and preglabellar field are concave distally and lack the convex border; pygidium has prominent posterior pleural bands extending to margin. The two genera are placed in Brachymetopidae, and a new diagnosis of that family given. Two species from Maine which occur with *Cordania macrobius* (Billings) are described: *Bojoscutellum? pompilius* (Billings), a scutelluid of uncertain generic affinities, and *Astycoryphe? junius* (Billings), a proetid with a weakly developed tropidium and *Astycoryphe*-like pygidium.

INTRODUCTION AND ACKNOWLEDGMENTS

DR. G. ARTHUR COOPER kindly invited me to describe the exceptional complete trilobite illustrated in pl. 51, fig. 11, 14, 15, 18. It is here regarded as a new species of *Cordania*, and shows clearly the dorsal facial sutures, including the widely divergent anterior branches. Since all previous accounts have stated that the facial sutures in species of this genus are fused or not discernible, it seemed desirable to reinvestigate the type and other species that have been referred to it. A new diagnosis of the genus is given, and the species here referred to it are all Lower Devonian in age. Certain species of Lower and Middle Devonian age that have been referred to *Cordania*, one of which clearly shows facial sutures, are referred to a new but closely related genus. Other Middle Devonian species that might belong to the new genus have not been considered here, since these trilobites are being studied by Dr. Erwin C. Stumm. The trilobites from the Lower Devonian of Square Lake, Maine, originally described by Billings (1869) but not studied since, include a species of *Cordania*. Considerable material from this locality is in the U. S. National Museum and in collections of the U. S. Geological Survey. In examining this I did not find much material of the cheirurid, phacopid, dalmanitid, or lichid described by Billings. However, there were good specimens of both the scutelluid and the proetid, and descriptions of some of the best of these specimens are included here because of their unusual interest and apparent relation to European forms.

I am indebted to Dr. G. Arthur Cooper, U. S. National Museum, Washington, D. C.



TEXT-FIG. 1—Some terms employed in the description of the pygidium; (a) based on *Mystrocephala pulchra;* (b) based on *Cordania macrobius.* 1–9, pleural furrows numbered successively; ab, anterior band of pleura; ahr, articulating half-ring; af, articulating furrow; f, facet; ip, interpleural furrow; pb, posterior band of pleura; rf, ring furrow of axis.

(USNM); and Mr. Clinton F. Kilfoyle, New York State Museum, Albany, N. Y., (NYSM), for permission to study and photograph material in their charge. The initials in parentheses precede the catalogue numbers of specimens in these institutions. Trilobita in material from Square Lake, Maine, were sent to me by Dr. Robert B. Neuman, U. S. Geological Survey, Washington, D.C. Dr. R. Goldring, University of Reading, England, supplied information regarding younger trilobites possibly related to *Cordania.* Professor H. K. Erben, Bonn University, West Germany, suggested the genus to which the Square Lake proetid may belong. Mrs. Karl F. Schuele made the enlargements from my negatives, and Miss Margaret Estey prepared text-figure 1.

TERMINOLOGY

The terminology used here follows that which I have employed in recent papers (1957 and references), with one addition. Many authors now number the lateral glabellar lobes and furrows from the posterior forwards, and confusion may arise if this is not understood. For brevity and to avoid such confusion I have employed the symbols suggested by Richter and Richter (1954, p. 7) and Goldring (1955, p. 31). The basal or posterior glabellar lateral lobe or furrow, (i.e. that adjacent to the occipital ring) is referred to as 1p, and those in front numbered successively forwards 2p, 3p, etc.—that is, second from the posterior, third from the posterior, etc.

Two terminologies are applied to the pleural regions of the pygidium, and the terms used here for brachymetopids and proetids are explained in text-figure 1. Pleural furrows are numbered from the anterior backward, the first running diagonally outward and backward from the articulating furrow (af). In front of the first pleural furrow is the first anterior band (ab), which bears the facet (f). Behind the first pleural furrow is the first posterior band (pb). The thorax of *Cordania* (pl. 51, fig. 14) appears to substantiate this interpretation, that is, the posterior pleural band of the thoracic pleura is the strongly convex band (as it is on the pygidium). The pleural furrow is deeper and broader than the interpleural furrow of the pygidium. In *Mystrocephala* n. gen. (pl. 53, fig. 16) the posterior pleural band is much more strongly convex than the anterior, and extends out to the margin, whereas the convex part of the anterior pleural band does not. The alternative terminology, employed by Goldring (1955), is to use the term "rib" for the strip lying between two pleural furrows, the rib being divided into two parts by a "rib furrow" (=interpleural furrow). This leads to calling what is here termed the posterior band the "anterior portion of the rib," and what is here termed the anterior band the "posterior portion of the rib" (cf. Goldring,

1955). The anterior band of the first pleura is called the "articulating half rib."

The pleural region of the scutelluid pygidium is here described as displaying ribs separated by grooves, without implication as to whether these grooves correspond to pleural or interpleural furrows.

SYSTEMATIC PALAEONTOLOGY

Family BRACHYMETOPIDAE Prantl and Přibyl, 1951

Diagnosis.—Cephalon semicircular in outline, convex, long genal spine; glabella narrowing forward, triangular basal lateral lobe isolated by deep, diagonal furrow 1p, lateral furrows 2p and 3p may be present; preglabellar field long (absent only in *Piltonia*), convex cephalic border in most genera, eye lobe situated far back and close to glabella, facial sutures opisthoparian, anterior branches widely divergent in some genera, sutures absent in *Brachymetopus;* rostral plate broad, hypostome unknown. Thorax of nine segments, pygidium relatively large, 10–13+axial rings; deep pleural furrows extend beyond fulcrum, posterior pleural band wider (exs.) and more convex than anterior, reaches to margin of pygidium and may be extended into spines. External surface of convex areas may be pitted, tuberculate or spinose.

Stratigraphical Range.—Lower Devonian to Carboniferous.

Discussion.—The genera included in this group (proposed as a subfamily) by its authors were the following: *Brachymetopus* M'Coy, 1847, *Brachymetopina* Reed, 1903 (a subjective synonym of *Brachymetopus* according to Goldring and Stubblefield, 1957, an interpretation disputed by Schmidt, 1958), *Cordania* Clarke, 1892, *Cheiropyge* Diener, 1897, *Namuropyge* R. and E. Richter, 1939, *Haploconus* Raymond, 1913 (a synonym of *Dimeropyge;* see Sinclair, 1946), *Tschernyschewella* Toll, 1899. Brachymetopinids were placed by Prantl and Přibyl in the family Otarionidae, and this family classified with the Proetidae in the superfamily Proetacea. Hupé (1953, p. 220; 1955, p. 210) used the family name Brachymetopidae, including in it *Brachymetopus, Cheiropyge,* and with question *Cordania.* Further, Hupé regarded the brachymetopids as allied to the proetids but not to the otarionids, a view with which Maksimova (1957) has expressed agreement. The "Treatise on Invertebrate Paleontology" (Moore, 1959) offers another arrangement. *Tschernyschewella* is removed to the Otarionidae, and *Panarchaeogonus* Öpik, 1937, is added to Brachymetopidae with question. The suprageneric classification, with some additions and changes of rank of taxa, is like that of Prantl and Přibyl. The new facts set forth herein suggest yet another arrangement, from which the diagnosis is derived. The reasons for this arrangement are as follows:

The diagnoses given below suggest that *Cordania* and *Mystrocephala* n. gen. are closely related. Perhaps most like them is *Tschernyschewella* (a new name for *Schmidtella* Tschernyschew, 1893, *non* Ulrich, 1892), type species *S. uralica* Tschernyschew, 1893, from the Lower Devonian of the Urals. The type species has a convex cephalon with a long genal spine, the glabella narrowing forward and having well defined, triangular basal lobes; the preglabellar field is long (sag.) and convex and there is a narrow, convex cephalic border. The anterior branches of the suture diverge less strongly forward than in *Mystrocephala.* Certain Carboniferous trilobites seem to be descendants of these Devonian forms. One is "*Cordania*" *gardneri* Mitchell, 1922, from Australia, new material of which is being studied by Drs. R. Goldring and K. S. W. Campbell. Information kindly supplied by Dr. Goldring shows that the Australian species does not belong in *Cordania,* though it has many features in common with it—the cephalon is convex with a narrow convex cephalic border, the glabella has prominent basal lateral lobes, preglabellar field is moderately long (sag.), the facial sutures have a course like that in *Tschernyschewella,* there are nine thoracic segments, and both these and the pygidium have prominent convex posterior pleural bands which reach the margin of the pygidium. The external surface is tuberculate, and there are small pits in the broad anterior and lateral cephalic border furrows. *Piltonia* Goldring, 1955, from the Lower Carboniferous of Britain and USSR, has the glabella with well defined triangular basal lobes, there is no preglabellar field, but a narrow cephalic border. The eye lobe is large, the anterior branches

of the suture slightly divergent. The pygidium is of similar form to that of *Cordania*, displaying more segments, but having the convex posterior pleural bands which extend out to the margin. External surface is tuberculate. *Brachymetopus* (Woodward, 1883–1884, p. 46–55, pl. 8; Goldring, 1955, p. 44–46, pl. 2, figs. 14,15, text-fig. 7; Maksimova, 1957) is perhaps least like any of the foregoing genera. The glabella has a triangular basal lobe, but is short (sag.), and the preglabellar field long. There is a narrow cephalic border. In the type and certain other species no sutures are associated with the large eye lobes. Nine thoracic segments; the pygidium is of similar form to that of *Piltonia*. Exterior surface tuberculate. Because these three Carboniferous genera have a number of characters in common with *Cordania* and *Mystrocephala* they are here placed in the family Brachymetopidae. I would not include either *Cheiropyge*, from the Permocarboniferous of India, or *Namuropyge* from the Carboniferous of Belgium, since the type species of each is a pygidium, neither of which appears particularly like any of those discussed above. I agree with Schmidt (p. O 408, footnote, in Moore, 1959) that *Panarchaeogonus* does not appear to belong here.

The relationships of the Brachymetopidae as here conceived are uncertain. As Maksimova (1957, p. 60–61) has pointed out, the nine thoracic segments and relatively large, well-segmented pygidium distinguish them from *Otarion* and its allies, and suggest a relationship with Phillipsiidae. However, this family includes only Carboniferous and Permian trilobites, and the cephalon is quite different from that of brachymetopids. Proetids, as well as otarionids, originate in the Middle Ordovician, but the Ordovician and Silurian species are not well known. More information is needed before an attempt may be made to trace the phylogeny of Proetacea.

Genus CORDANIA Clarke, 1892

Type species.—By original designation, *Phaëthonides cyclurus* Hall and Clarke, 1888.

Diagnosis.—Convex glabella tapering forward, occipital ring and large basal glabellar lobe well-defined, furrow 2p faint. Cheek and preglabellar field broad, wide convex border, long librigenal spine broad at base; small eye lobe situated on inner, convex part of cheek, opposite anterior part of basal glabellar lobe, anterior branches of suture strongly divergent, in mid-part at 60–90° to sagittal line, sinuous course. Rostral plate broad (tr.), hypostome unknown. Thorax in two species of nine segments, pleural furrow extends beyond fulcrum, posterior pleural band broader (exs.) and more convex than

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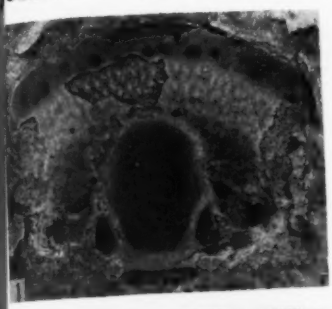
EXPLANATION OF PLATE 51

FIGS. *1–7,9,10,12,13,19—Cordania cyclurus* (Hall and Clarke, 1888), New Scotland limestone, Clarkesville, Albany County, N. Y. *1,4*, lectotype, external mould of cranidium, fig. *4* photographed under alcohol, NYSM 4215, ×3. *2,3,6*, latex cast from lectotype, dorsal, anterior, right lateral views, ×3. *5,7,9*, internal mould of incomplete cranidium, NYSM 4213, original of Hall and Clarke, pl. 24, figs. 26,26a, dorsal, right lateral, anterior views, ×4. *10,12,13*, incomplete pygidium with some exoskeleton adhering, NYSM 4214, original of Hall and Clarke, pl. 24, fig. 28, posterior, left lateral, dorsal views, ×4. *19*, external mould of pygidium with some exoskeleton adhering, NYSM 4214, original of Hall and Clarke, pl. 24, fig. 27, ×4.

8,11,14–18—Cordania falcata n.sp., Haragan formation, Murray County, Oklahoma.

11,14,15,18, holotype, USNM 136468, almost complete exoskeleton, anterior, dorsal, left lateral, posterior views, ×3. *8,17*, enrolled incomplete exoskeleton, USNM 137695, left lateral, dorsal views, ×3. *16*, incomplete enrolled exoskeleton, USNM 137694, oblique exterior view showing doublure of left side of cephalon and connectivie suture, ×3.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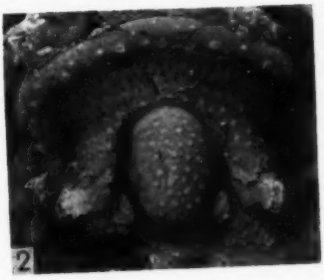
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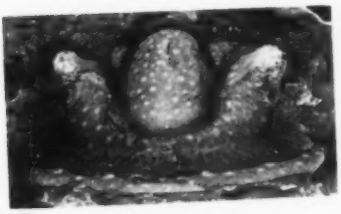
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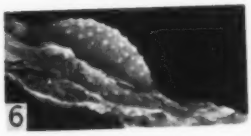
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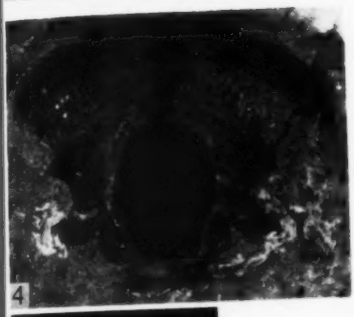
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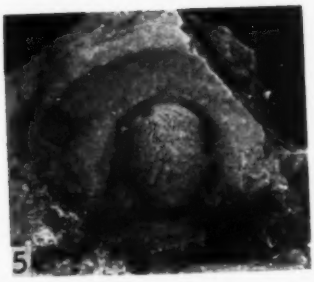
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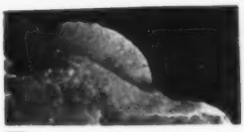
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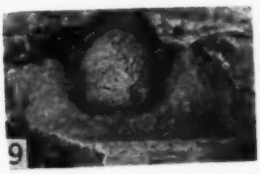
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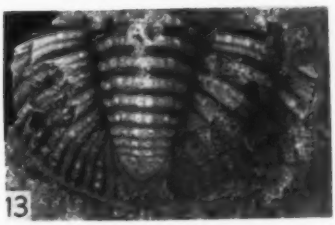
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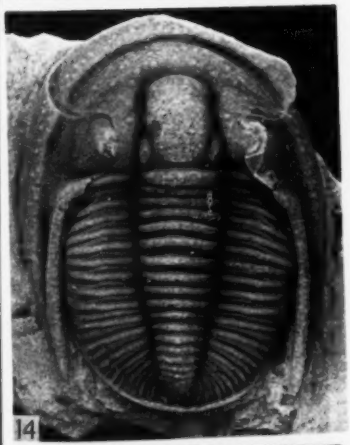
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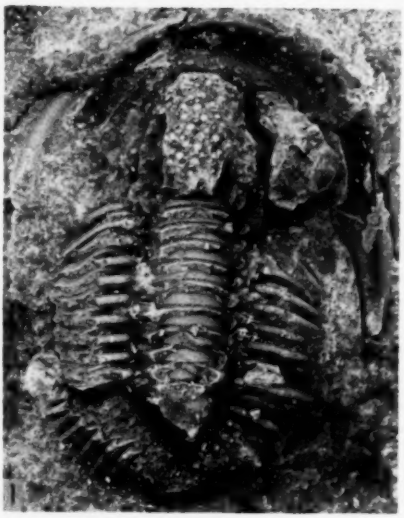
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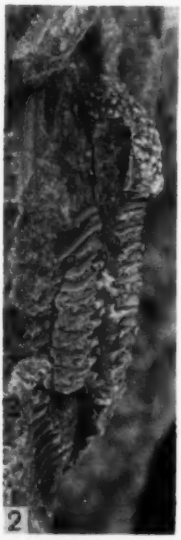
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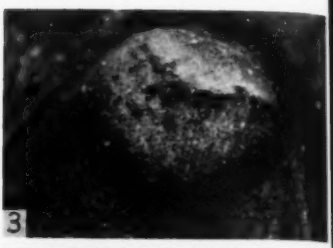
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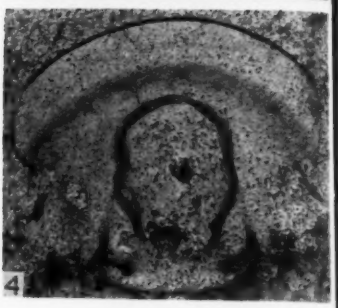
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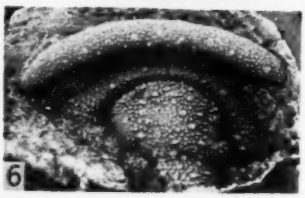
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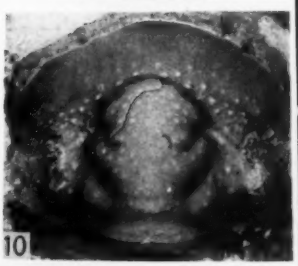
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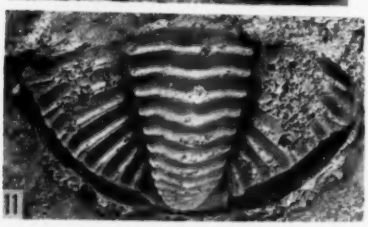
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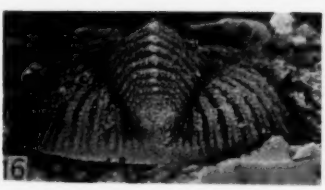
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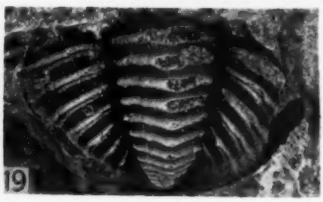
19

anterior. Pygidium sub-semicircular in outline, convex axis with about ten rings, pleural region lacking border or border developed as a narrow rim, eight to nine pairs of pleural furrows, flanked by low anterior bands and stronger posterior pleural bands, all extending to margin. External surface pitted, tubercles on convex parts of cephalon, axial rings and posterior pleural bands; terrace lines on margin and doublure.

Stratigraphical Range.—Early Lower Devonian (Helderberg and Deerpark).

CORDANIA CYCLURUS (Hall and Clarke, 1888)
Pl. 51, figs. 1–7,9,10,12,13,19

Lectotype (here selected).—NYSM 4215, original of Hall and Clarke, pl. 25, fig. 11, incomplete external mould of a cranidium with thin layer of exoskeleton adhering, New Scotland limestone, Clarkesville, Albany county, N. Y.

Other Material.—NYSM 4213, original of Hall and Clarke, pl. 24, figs. 26,26a, incomplete internal mould of a cranidium; NYSM 4214, originals of Hall and Clarke, pl. 24, figs. 27,28, incomplete pygidia, not counterparts, one an internal mould with exoskeleton adhering, the other an external mould with exoskeleton adhering on left side, and some layers of the exoskeleton on the right side. All from New Scotland limestone, Clarkesville, Albany county, N. Y. The example showing the cephalon and pygidium "in juxtaposition" (Hall and Clarke, 1888, p. 139) is not preserved in the New York State Museum collections.

Description.—Lectotype cranidium of length (sag.) 10.7 mm. Occipital ring short (sag.), convex, sloping forward to broad, deep occipital furrow. In front of this furrow glabella narrows progressively forward to rounded anterior margin; axial furrows broad and deep, preglabellar furrow equally broad but shallower, especially medially; length (sag.) of glabella two-thirds that of cranidium; glabella is convex, and highest point (lying in a transverse line with anterior part of palpebral lobes) is as high, or slightly higher than, occipital ring in mid-line. Diagonal basal lateral glabellar furrow as broad and deep as axial furrow and extending from this furrow to occipital furrow, isolating a convex basal lobe which is sub-oval in outline. In the steep lateral slope of the glabella, at a distance in front of the basal

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EXPLANATION OF PLATE 52

FIGS. *1,2*—*Cordania gasepiou* Clarke, 1908, Lower Devonian, Grande Grêve limestone, Quebec. Holotype, NYSM 9695, fragmentary exoskeleton, original of Clarke, 1908 pl. 9, fig. 9, dorsal, left lateral views, ×6.

3,5—*Cordania falcata* n.sp., Lower Devonian, Haragan formation, Oklahoma. *3*, left eye lobe of original of Pl. 51, figs. 8,17, showing small facets, ×20. *5*, incomplete enrolled exoskeleton, USNM 137694, dorsal view, ×3.

4—*Cordania* sp. Lower Devonian, Birdsong shale, Tennessee, USNM 137696, internal mould of cranidium, ×3.

6–9,11,13,14,16–19—*Cordania becraftensis* Clarke, 1900, Lower Devonian, Glenerie limestone, Hudson, N. Y. *6*, latex cast of incomplete external mould of cranidium, NYSM 4212, original of Clarke, pl. 2, fig. 23, ×3. *7–9*, lectotype, incomplete internal mould of cranidium, right lateral, dorsal, anterior views, NYSM 4210, original of Clarke, pl. 2, fig. 21, X4-½. *11,14*, internal mould of pygidium, dorsal, posterior views, NYSM 4207, original of Clarke, pl. 2, fig. 17, ×3. *13,16,17*, latex cast of external mould of pygidium, dorsal, posterior, left lateral views, NYSM 4208, ×4. *18,19*, internal mould of pygidium, left lateral, dorsal views, NYSM 4208, original of Clarke, pl. 2, fig. 19, ×3

10,12,15—*Mystrocephala rara* (Stumm, 1953), Middle Devonian, Alpena County, Michigan. Holotype, USNM 117869, incomplete cranidium, dorsal, anterior, right lateral views, ×4.

lateral furrow about equal to the length (exs.) of the basal lobe, is a faint depression suggesting lateral glabellar furrow 2p. In front of furrow 2p the axial furrow deepens towards its junction with the preglabellar furrow. Preglabellar field long (sag. and exs.), sloping gently forward and merging in a concave slope into the broad anterior border furrow; anterior border wide and gently convex. Laterally preglabellar field merges into fixed cheek. Palpebral lobe short (exs.), length less than that of basal glabellar lobe, standing high above cheek and situated opposite anterior part of this basal lobe; palpebral lobe without rim and sloping steeply inward. Inner part of fixed cheek, beside and in front of palpebral lobe, convex, outer part broadly concave with gently convex border. Anterior branch of suture runs forward and outward in an 'S' curve—in detail the course is at first in ward from the palpebral lobe, then curving to run almost transversely outward a short distance in front of the palpebral lobe, continuing in a broad curve through 90° or more to the antero-lateral margin (pl. 51, fig. 4). In the lectotype the edge of the cranidium in the outer part of the cheek is broken on both sides, but I consider the sutural boundary to be preserved on each side where it crosses the cephalic border—in a curve which is now running forward and slightly inward at the outer margin. Postero-lateral part of glabella and cheek, and course of posterior branch of suture, not preserved in the lectotype.

External surface of convex parts of exoskeleton of lectotype bearing large, scattered tubercles. Largest tubercles on median part of anterior border. Concave area of fixed cheek and preglabellar field bears extremely faint pattern of shallow depressions, these depressions arranged quincuncially and elongated in a radial direction.

The second specimen (pl. 51, figs, 5,7,9) is less complete, of length (sag.) 6.7 mm., and showing the same features. The short, shallow depression representing lateral furrow 2p is more clearly visible, and in front of it is a shorter and fainter depression, opposite the deep anterior part of the axial furrow, possibly representing lateral furrow 3p. Palpebral lobe not preserved, but on the left side the course of the outer part of the anterior branch of the suture may be followed.

Internal mould of pygidium (pl. 51, figs. 10,12,13) of length (sag.) 6.8 mm., pleural lobes broken distally and on right side exoskeleton stripped off and external mould of doublure revealed. External mould of pygidium (pl. 51, fig. 19) of almost same length, pleural lobes incomplete laterally. Outline of pygidium subsemicircular, convex, with convex axis tapering posteriorly and terminating at inner edge of doublure. Axis of 10 distinct rings marked off by ring furrows that are shallow and broad medially, but become narrower and deep distally. Tenth ring is on steep slope of tip of axis. Rings slightly inflated distally. Pleural regions horizontal beside anterior half of axis, outside these areas sloping steeply to lateral and posterior margins. No convex border, an indentation concentric to margin lies above inner edge of doublure and thus posteriorly lies against tip of axis. Pleural furrows curve outward and back, and are directed successively more strongly backward; eight pleural furrows may be seen, each successively shallower, the eighth faint and directed backward. Interpleural furrows shallower and narrower than pleural, except distally; posterior pleural bands slightly more convex than the anterior; furrows and bands extend out to the margin. Between the eighth pair of pleural furrows may be seen two further pairs of faint pleural bands, the inner, posterior of which runs beside the tip of the axis and behind the axis encloses a faint median post-axial rib. External surface bearing tubercles on rings and bands. On the axial rings four pairs of tubercles, the inner pair close together at the mid-line, the outer pair situated on the inflated distal region. From the fourth axial ring posteriorly the median pair are the most prominent, and become farther apart on successive rings. On the pleural regions larger tubercles occur principally in rows on the posterior pleural bands, and are spaced fairly widely except for a pair close together on the outer part beyond the indentation. The tubercles aid considerably in outlining the course of these bands. A fine-grained granulation is also present on the bands and rings. Dou-

blure bent up to lie close against dorsal exoskeleton.

CORDANIA FALCATA n. sp.
Pl. 51, figs. 8,11,14–18; pl. 52, figs. 3,5.

Holotype.—USNM 136468, exoskeleton, exposed from dorsal side, Haragan formation, White Mound, NW ¼, NE¼, sec. 20, T.2S., R.3E., Murray Co., Oklahoma. H. L. Strimple collection.

Other material.—USNM 137694–5, and unnumbered, three incomplete enrolled exoskeletons, two incomplete cephala, same horizon and locality.

Description.—Holotype of length 19.2 mm., maximum width of cephalon (at posterior margin) 14.7 mm., pygidium of length 5.3 mm., maximum width at anterior m rgin 10.2 mm.

Cranidium differentiated from that of *Cordania cyclurus* by convex preglabellar field and anterior area of fixed cheek, which descend to narrow anterior border furrow, anterior border broad and convex (compare pl. 51, fig. 15 with pl. 51, fig. 6). Because of differences in the mode of preservation it is difficult to compare other features, but the occipital furrow in *C. falcata* appears to be shallower and narrower (sag. and exs.), and the basal lateral glabellar and axial furrows are less deep. Large tubercles are scattered over the external surface of preglabellar field and anterior area of fixed cheek of *C. falcata* (pl. 51, figs. 14,17), such tubercles are present in *C. cyclurus* only immediately in front of the preglabellar furrow and on the fixed cheek beside the glabella (pl. 51, figs. 1,2); closely spaced and quincuncially arranged pits are present in both species (pl. 51, fig. 2; pl. 52, fig. 5).

Cheek highest at point in line with, and close to, anterior part of basal glabellar lobe; eye lobe at highest point, cheek sloping steeply down from eye lobe. Eye surface (pl. 52, fig. 3) with many tiny facets arranged in diagonal lines. Posterior border of similar width (exs.) and convexity to occipital ring, inner part directed transversely, behind eye lobe deflected slightly backward, and at two-thirds width of cheek curving sharply to merge with internal border of librigenal spine. Posterior border furrow moderately deep, librigenal spine broad (tr.), long, reaching back to point opposite tip of pygidial axis; broad external border continuous with lateral cephalic border, narrower internal border, depression between these borders narrowing and disappearing distally. Cephalic doublure as broad as border, convex, inner part curled up vertically. Anterior branch of suture much as in *C. cyclurus*, curve out from palpebral lobe sharp, mid portion directed transversely, reaching anterolateral margin at point in line (exs.) with internal border of librigenal spine, then running diagonally inwards a short distance across outermost part of doublure to meet rostral suture at oblique angle. Rostral plate (pl. 51, fig. 16) of width (tr.) about equal to distance between palpebral lobes, defined by backwardly converging connective sutures, posterior part curved up vertically. Hypostome unknown. Posterior branch of suture runs outward and backward in 'S' curve, cutting posterior margin at about half width of cheek.

Thorax of nine segments, convex axis tapering backward. Convex rings only slightly inflated distally. Inner part of pleura flat, outer part bent gently down, tip rounded. Narrow, deep pleural furrow extends beyond fulcrum, posterior band broader and more convex than anterior. Facet large, especially on narrower (tr.) anterior segment where it fits beneath posterior cephalic border and base of librigenal spine.

Pygidium differing from that of *C. cyclurus* in the less steeply sloping outer parts of the pleural regions and in exhibiting a narrow, convex border which is most prominent posteriorly.

External surface with close-spaced quincuncially arranged pits, these pits prominent on the outer part of the cheek. Tubercles scattered on glabella, cheek, cephalic borders, axial rings and posterior pleural bands; on glabella close spaced, on anterior part of cheek and preglabellar field large and widely spaced, median and paired on occipital ring and axial rings. Strong terrace lines on cephalic margin and doublure.

Discussion.—Other trilobites from the Haragan formation have recently been listed by Amsden (1956a, p. 46–49; 1956b, p.

138). In the U. S. National Museum there is also a proetid and *Otarion* sp.

Cordania macrobius (Billings, 1869)
Pl. 53, figs. 1–14,17,18,20,21;
text-fig. 1b.

Material.—USNM 137697–8 and unnumbered cranidia, fragments of free cheeks, pygidia, from Lower Devonian of New Scotland limestone age, Square Lake, Aroostock County, Maine. Coll. O. Nylander; P. E. Cloud.

Description.—Axial, occipital and basal glabellar furrows shallower than in either *C. cyclurus* or *C. falcata*, and slopes down to them consequently gentler. Preglabellar field and anterior parts of free cheeks gently convex and outward-sloping—less convex than those of *C. falcata* but more steeply sloping than the corresponding concave area in *C. cyclurus* (compare pl. 53, fig. 3 with pl. 51, figs. 6,15). Anterior border of cranidium convex, defined by broad, deep border furrow, anterior slope vertical. Position and elevation of palpebral lobe as in *C. cyclurus* and *C. falcata*, course of sutures similar except that posterior branch has straight, diagonally directed course, rather than 'S' shape of *C. falcata*. Free cheek as in *C. falcata*, long librigenal spine with broad outer and narrower internal borders, depression between them dying out distally. Doublure of free cheek (pl. 53, figs. 10,12) curled under so that it is directed vertically beneath border, then inmost part flexed abruptly to slope upward and inward beneath outer part of cheek; the border is thus subcylindrical in cross-section. Pygidium like that of *C. cyclurus*, the outer part of the pleural region more steeply sloping than that of *C. falcata* and exhibiting the narrow, slightly raised border, into which the anterior and posterior pleural bands run. Both Billings (1869, p. 123) and Hall and Clarke (1888, p. 139) described the external surface of the cranidium as punctate. This pitted appearance is exhibited by moulds of the internal surface of the exoskeleton (pl. 53, figs. 4,5), which also exhibit an extremely faint depression on the side of the glabella at about one-third the length—lateral furrow 2p. Pitting is also seen on internal moulds of the free cheek (pl. 53, fig. 11). It is coarsest on the cephalic border, and on the preglabellar field and adjacent areas the pits are quincuncially arranged and separated by faint, anastomosing radial ridges. In one cranidium which has the external surface of the exoskeleton preserved (pl. 53, figs. 1–3) close-spaced pits are present everywhere except in the furrows and are largest in, and adjacent to, the border furrow. An oval smooth area indicates the position of lateral furrow 2p. Small tubercles are scattered on the glabella and anterior border, a few larger, faint tubercles on the preglabellar area. The smaller tubercles of glabella and anterior border also distinguish this species from *C. cyclurus* and *C. falcata*. When the external surface of the pygidial exoskeleton is preserved (pl, 53, figs. 17,20,21) tubercles are visible on axial rings and both pleural bands.

Hall and Clarke (1888, p. 139) do not seem to be correct in stating that *C. macrobius* has a longer glabella and fewer axial rings in the pygidium than *C. cyclurus*.

Cordania becraftensis Clarke, 1900
Pl. 52, figs. 6–9,11,13,14,16–19

Cordania hudsonica Clarke, 1900, p. 24, Pl. 2, figs. 17,18.

Lectotype (here selected).—NYSM 4210, incomplete internal mould of cranidium, original of Clarke, 1900, pl. 2, fig. 21, Oriskanian (Glenerie limestone), Becraft Mountain, Hudson, N. Y.

Other Material.—Originals of Clarke, 1900, pl 2, as follows: NYSM 4211, incomplete internal mould of cranidium, original of fig. 22; 4212, incomplete external mould of cranidium, original of 23; 4208, internal and external moulds respectively of 2 pygidia, the former the original of fig. 19; 4209, external mould of pygidium, original of fig. 20; 4221, incomplete internal mould of pygidium, original of fig. 18, first placed in *C. hudsonica*, but later (Clarke, 1908, p. 136) referred to *C. becraftensis;* 4207, internal mould of pygidium, original of fig. 17, and the holotype of *C. hudsonica;* all from Oriskanian (Glenerie limestone), Becraft Mountain, Hudson, N. Y.

Description.—Preglabellar field relatively short (sag. and exs.), convex immediately in front of preglabellar furrow but greater part deeply concave and passing forward into broad, convex border. The cranidium is

much like that of *C. cyclurus*, except that the preglabellar field is shorter and more steeply sloping, and the anterior branch of the suture diverges at about 65° from the sagittal line. External surface (pl. 52, fig. 6) of convex areas bearing close-spaced small, and scattered large, tubercles; smooth area indicates lateral furrow 2p.

Pygidium subsemicircular in outline, convex; axis convex, tapering backward to rounded tip, nine rings outlined by ring furrows which become progressively shallower posteriorly, each ring curving back slightly at the midline. Three additional rings indicated on the posterior tip by transverse lines of tubercles. Pleural regions horizontal close to anterior part of axis, posterolaterally steeply sloping, approaching vertical behind tip of axis. Eight pairs of deep pleural furrows, directed progressively more strongly backward; shallow interpleural furrows, posterior pleural band wider and more convex than the anterior. Pleural bands following the eighth pleural furrow run backwards and inwards close beside the tip of the axis. Pleural furrows and bands become shallower and lower respectively on the steeply sloping border; doublure convex and extending beneath this border. External surface of axial rings bearing small, sharp, close spaced tubercles, in the midline a short, blunt, backwardly-directed spine; similar tubercles on pleural ribs.

The holotype of *Cordania hudsonica* Clarke, 1900, is an internal mould of a pygidium (pl. 52, figs. 11,14) and indistinguishable from specimens (pl. 52, figs. 13, 16–19) originally placed in *C. becraftensis* by Clarke.

The steepness of the outer part of the pleural regions distinguish the pygidium of this species from all others known.

CORDANIA GASEPIOU Clarke, 1908
Pl. 52, figs. 1,2

Holotype.—NYSM 9695, fragmentary exoskeleton exposed from dorsal side, original of Clarke, 1908, pl. 9, fig. 10, Grande Grêve limestone, Lehuquet's Cove, Grande Grêve, Quebec, Canada.

Other Material.—The original of Clarke's 1908, pl. 9, fig. 9, said by Kilfoyle, 1954, p. 506, to be in the U. S. National Museum, could not be found up to the time of writing.

Discussion.—The holotype is too poorly preserved for complete description, but so far as can be seen it displays the characters of *Cordania*. Glabella convex, tapering forward, with large triangular basal lateral lobe set off by deep diagonal furrow. Preglabellar field long (sag. and exs.), gently convex and sloping forward to broad, deep border furrow; anterior cephalic border broad, convex. Anterior branch of suture directed outward and slightly forward at a high angle to the midline. Free cheek with broad, convex lateral border and long librigenal spine, latter with median depression between convex internal and external borders. Thorax of nine segments, deep pleural furrow and strongly convex, wide (exs.) posterior pleural band. Pygidium of typical outline and convexity, deep pleural furrows, shallow interpleural furrows, posterior band more convex than anterior, bands and furrows extending out close to margin. Outer parts of pleural region gently sloping, unlike that of *C. becraftensis*. The gentle convexity and slope of the preglabellar field, the strongly raised anterior cephalic border, and the deep concavity separating them, distinguish this species from either *C. macrobius* or *C. falcata*, and recall the characters of *C. cyclurus;* the latter species does not have, however, so strongly raised an anterior border.

CORDANIA sp.
Pl. 52, fig. 4

Material.—USNM 137696, internal mould of a cranidium in siltstone, Birdsong shale, Pickwick Dam, T.V.A. Pickwick—Counce Quadrangles, Hardin Co., Tenn.

Description.—Glabella narrowing forward, well-defined occipital ring, large triangular basal lateral lobe, faint furrow 2p. Preglabellar field short (sag. and exs.) as in *C. becraftensis*, anterior border broad, convex. Palpebral lobe opposite anterior part of basal lateral glabellar lobe, anterior branches of facial suture widely divergent. Large tubercles scattered on anterior border.

MYSTROCEPHALA n. gen.

Type species.—*Cordania pulchra* Cooper and Cloud, 1938.

Diagnosis.—Cephalon differs from that of *Cordania* in that lateral glabellar furrow 2p is deeper and longer, and lateral glabellar

lobe 2p is gently convex; cheek and preglabellar field is concave distally with upturned edge, and lacks the broad, convex border; anterior branches of sutures strongly divergent (at 70° to mid-line, i.e. less than in some species of *Cordania*). Rostral plate and hypostome unknown.

Thorax unknown. Pygidium differs from that of *Cordania* in that anterior pleural bands, which are present on the first six or seven segments, are low and do not extend on to outer parts of pleural regions, whereas posterior pleural bands are prominent and extend to margin.

Stratigraphical Range.—Late Lower Devonian (Onesquethaw) to late Middle Devonian (Taghanic).

MYSTROCEPHALA PULCHRA (Cooper and Cloud, 1938)
Pl. 53, figs. 15,16,19,22–26; pl. 54, figs. 1–5; text-fig. 1a.

Holotype.—USNM 95198a, cephalon, left free cheek displaced a short distance posteriorly, preserved in brown granular limestone, original of Cooper and Cloud, 1938, pl. 55, figs. 28,34; Devonian, first hollow south of Kritesville, SE ¼, NE ¼, sec. 20, T.11 S., R.2 W., Hardin quadrangle, Calhoun Co., Illinois. These strata are placed by Cooper *et al.* (1942) in the upper Middle Devonian Taghanic stage.

Paratypes.—USNM 95198c, cranidium; 95198d,e, pygidia; same locality and horizon, originals of Cooper and Cloud, 1938, pl. 55, figs. 29, 31–33.

Other Material.—USNM 95214, additional cranidia and pygidia, same locality and horizon.

Description.—Glabella of maximum width across occipital ring and basal lateral glabellar lobes, in front of these narrowing considerably, outlined by shallow axial and faint preglabellar furrows; axial furrow deepest beside occipital ring, glabellar lobe 2p and frontal lobe. Occipital furrow deep behind basal glabellar lobe (described by Cooper and Cloud as the "occipital" lobe), latter trapezoidal in outline, defined anteriorly by deep, diagonal glabellar furrow 1p which is connected by a broad, shallow depression to the occipital furrow. Lateral glabellar furrow 2p parallel to 1p, deepest close to axial furrow, shallowing inward; glabellar lobe 2p gently convex. Inner part of cheek convex, outer part concave, merging with broad (sag. and exs.) preglabellar field, a narrow part of which is gently convex in front of preglabellar furrow, the broader anterior part being concave; ill-defined narrow border to cheek and preglabellar area along upturned edge; posterior border widest (exs.) on fixed cheek, narrower distally, librigenal spine broad at base, tapering, median part between narrow borders concave. Midpoint of large eye lobe opposite glabellar furrow 1p. anterior branch of suture runs outward and forward at about 70° to sagittal line in a slightly sinuous course, posterior branch runs diagonally outward at about 45° to sagittal line; eye surface with many tiny facets faintly indicated on external surface (pl. 53, fig. 25). Faint eye ridge visible (pl. 54, fig. 1) where it descends to axial furrow opposite outer end of glabellar furrow 2p. Doublure of cheek (pl. 53, fig. 26; pl. 54, fig. 3) broad, extending beneath librigenal spine, anterolaterally extending two-thirds of distance beneath cheek in toward eye lobe, and anteriorly reaching inward close to preglabellar furrow. Anterior branch of suture runs along margin half-way in to midline, connective suture as seen on right free cheek of one specimen (pl. 54, fig. 3) appears to run at first inward, then curves to run backward and outward across doublure. If this interpretation is correct, then rostral plate is narrowest at about one-third its length (sag.). Hypostome unknown. External surface of cephalon pitted, pits tiny on glabella, larger on cheek and preglabellar area, large and small tubercles scattered on glabella (except in furrows), convex part of cheek and preglabellar area, and posterior border. Terrace lines on doublure and margin of cephalon.

Thorax unknown.

Convex axis of pygidium divided into ten axial rings, two additional rings faintly indicated on vertical slope of tip. Pleural region convex, outer part steeply sloping to flattened border area which is broadest posteriorly. Pleural region (text-fig. 1a) subdivided by eight strong bands which run out to the margin, a faint ninth band (Pl. 54, fig. 5) may be present behind the axis and

close to the midline; these bands are the posterior (not anterior, as stated by Cooper and Cloud, 1938, p. 458) pleural bands, and in front of each is the pleural furrow, in front of this furrow a narrower, lower anterior pleural band. The anterior pleural bands are visible on the first six or seven segments, but extend only part way down the slope of the pleural region. Doublure convex ventrally, extending inward under concave outer part and to tip of axis. External surface pitted except on crests of axial rings and pleural bands; large median and two lateral pairs of tubercles on axial rings; on proximal portion of posterior pleural bands four or five large tubercles. Doublure and margin bearing terrace lines.

MYSTROCEPHALA RARA (Stumm, 1953)
Pl. 52, fig. 10,12,15

Holotype.—USNM 117869, cranidium, Middle Devonian, Traverse group, Four Mile Dam limestone, exposures on banks and in bed of Thunder Bay river below Four Mile dam, ¼ mile south of center sec. 7, T.31 N., R. 8 E, Alpena county, Michigan.

Description.—Cranidium preserved as a mould of internal surface of exoskeleton with only a fragment of exoskeleton adhering. The lobe described by Stumm (1953, p. 124–5) as "occipital" is here termed basal or lateral glabellar 1p.

Cranidium differs from that of *M. pulchra* in that median part of occipital furrow, and depression connecting inner end of glabellar furrow 1p to occipital furrow, are shallower; glabellar furrow 2p is deeper and bifurcates at inner end; anterior part of fixed cheek and preglabellar field are less strongly upturned near border and thus appear less deeply concave (compare pl. 52, fig. 15, with pl. 53, fig. 23). The low eye ridge runs forward into the axial furrow opposite the outer end of glabellar furrow 2p.

MYSTROCEPHALA VARICELLA (Hall and Clarke, 1888)
Pl. 54, figs. 6–10,12.

Lectotype (here selected).—NYSM 4223, counterpart moulds of incomplete cranidium, flattened and cracked, original of Hall and Clarke, 1888, pl. 24, figs. 29,29a, Onondaga limestone, Canandaigua, N. Y.

Other Material.—NYSM 4224, 4225, incomplete internal moulds of cranidium and pygidium, originals of Hall and Clarke 1888, pl. 24, figs. 30,30a, and 31, Onondaga limestone, Canandaigua, N. Y.

Description.—Cranidium extremely like that of *M. pulchra*—glabella with triangular basal lobe defined by deep lateral furrow 1p, shallower diagonal lateral furrow 2p, frontal lobe more inflated, giving a more convex profile (compare pl. 54, fig. 10 with pl. 54, fig. 2). Preglabellar field broad and strongly recurved. Palpebral lobe situated opposite glabellar furrow 1p, anterior branch of facial suture strongly divergent. External surface bearing scattered large tubercles on glabella, fixed cheek beside glabella, and preglabellar field immediately in front of preglabellar furrow; the position of these tubercles being almost identical with those of *M. pulchra* (compare pl. 54, fig. 12 with pl. 54, fig. 1). Outer part of preglabellar field and fixed cheek bearing close-spaced, irregularly disposed pits.

Pygidium having the same number of axial rings, pleural furrows and ribs as *M. pulchra*, the strong posterior pleural bands continuing out to the margin; pygidium distinguished from the type species by the gentler postero-lateral slope of the pleural regions and the longer (sag.) portion behind the axis.

Particularly in the form of the preglabellar field and anterior part of the fixed cheek, this species appears to be more closely related to the type than to *M. rara*.

Family SCUTELLUIDAE R. and E. Richter, 1955

(I prefer to accept the emended spelling of this name proposed by the Richters, rather than revive an old name, as suggested by Moore, 1959, p. O 367.)

Genus BOJOSCUTELLUM Šnajdr, 1958
BOJOSCUTELLUM ? POMPILIUS (Billings, 1869)
Pl. 54, figs. 13–16,20,21,24,25

Material.—USNM 137699a–d, cranidia, free cheek, incomplete pygidia, from Lower Devonian of New Scotland limestone age, Square Lake, Aroostock County, Maine. Collected P. E. Cloud, 1941.

Description.—In Billings' original illus-

tration (1869, fig. 25) the cephalon was drawn from a Canadian specimen. The present illustrations are thus the first to be published of topotype material. Glabella narrowest adjacent to occipital furrow, expanding in front of here, axial furrows fading out beside anterior lobe, which is not defined by any preglabellar furrow but curves downward over margin of cephalon. Areas of muscle insertion, which include the lateral glabellar furrows, are smooth and slightly depressed, and appear as darker areas in the photograph (pl. 54, fig. 25). An area situated in anterolateral corner of occipital ring, 1p largest, horseshoe shaped, situated a short distance in front of occipital furrow, 2p smaller, subtriangular in outline, and situated a short distance from the median glabellar tubercle, 3p smallest, elongate transversely and situated a short distance anterolaterally from 2p; an additional area on the fixed cheek adjacent to the axial furrow immediately in front of the occipital furrow; axial furrow deepest adjacent to this area. Eye lobe opposite preoccipital portion of glabella, large, elevated and situated in line (exs.) with the anterolateral part of the anterior glabellar lobe. Eye surface (pl. 54, fig. 20) covered with many minute facets arranged in diagonal lines. Anterior branch of suture curves forward and outward in a sigmoidal course, posterior branch curves backward and outward, runs for a short distance parallel to the posterior border furrow, then curves in a semicircle across the posterior border; posterior border furrow ends a short distance inside the posterior branch of the suture. Inner part of free cheek gently convex, outer part gently concave, no borders or border furrows, short blunt librigenal spine. Outer edge of free cheek and librigenal spine sharp—there being an acute angle between the dorsal surface and the doublure. This sharp edge continues across the anterior branch of the suture on to the fixed cheek and becomes rounded at the distal edge of the anterior glabellar lobe. External surface with raised anastomosing lines, concentrically arranged on preoccipital portion of glabella and on fixed cheek, elsewhere on glabella and inner part of free cheek running transversely or subparallel to the anterolateral margin; on free cheek as lines approach lateral margin they curve forward to run subparallel to margin and then abruptly backward at margin.

Pygidium with short triangular axis, posteromedian part convex, posterior tip projecting upward and backward; subdivided transversely only by articulating furrow,

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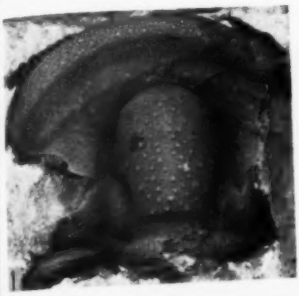
EXPLANATION OF PLATE 53

FIGS. *1–14,17,18,20,21—Cordania macrobius* (Billings, 1869), Lower Devonian, Square Lake, Maine. *1–3*, incomplete cranidium, exoskeleton adhering, dorsal, anterior, left lateral views, USNM 137697a, ×3. *4,5*, internal mould of incomplete cranidium, dorsal, anterior views, USNM 137697b, ×3. *6,7*, incomplete cranidium, internal mould, dorsal, anterior views, USNM 137697c, ×3. *8,9*, incomplete cranidium, dorsal, left lateral views, USNM 137697d, ×6. *10*, right free cheek, border removed to show external mould of doublure, USNM 137697e, ×3. *11*, left free cheek, internal mould, some exoskeleton adhering, USNM 137697g, ×3. *12*, right free cheek, border partly broken away revealing external mould of doublure, USNM 137697f, ×3. *13,14,18*, incomplete pygidium, exoskeleton adhering, dorsal, posterior, left lateral views, USNM 137698a, ×3. *17,20,21*, incomplete pygidium, exoskeleton adhering, dorsal, posterior, right lateral views, USNM 137698b, ×3.

15,16,19,22–26—Mystrocephala pulchra (Cooper and Cloud, 1938), Devonian, Calhoun County, Illinois. *15,22,23,25*, holotype, incomplete cephalon, USNM 95198a, dorsal, anterior, right lateral views, ×4; right eye lobe, ×20. *16,19,24*, pygidium, dorsal, posterior, left lateral views, USNM 95198d, ×6. *26*, cephalon, free cheeks displaced, exposed from ventral side, oblique view showing doublure of left free cheek, USNM 95214, ×4.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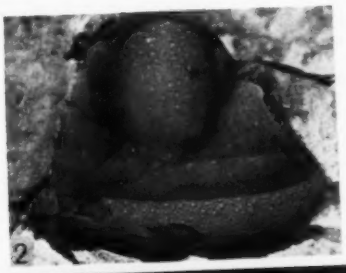
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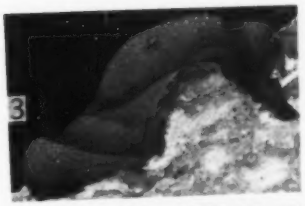
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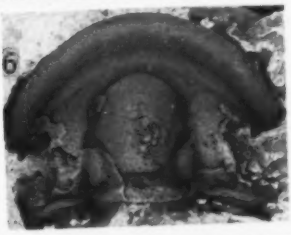
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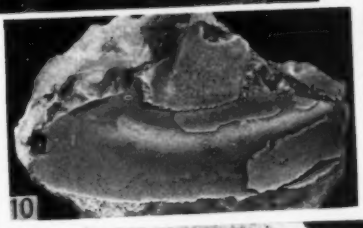
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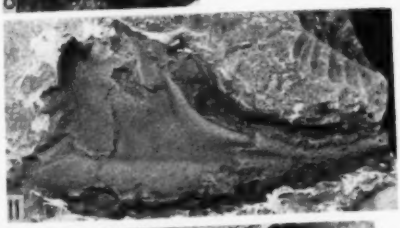
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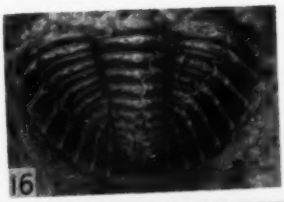
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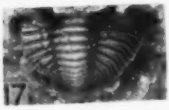
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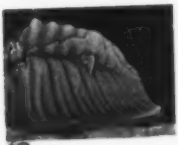
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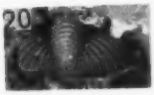
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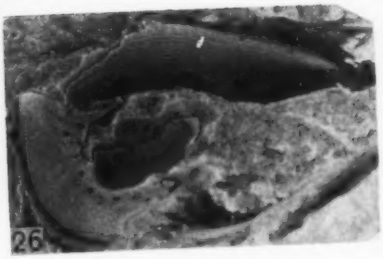
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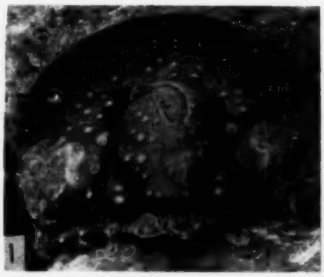
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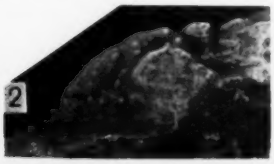
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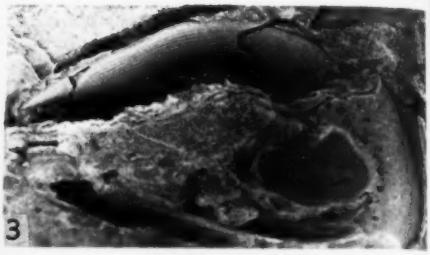
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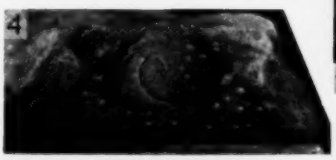
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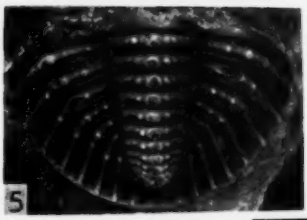
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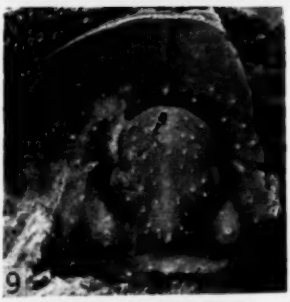
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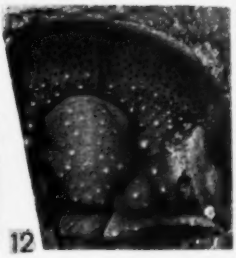
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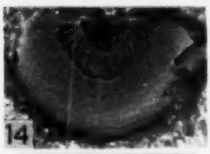
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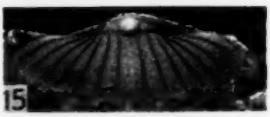
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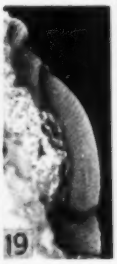
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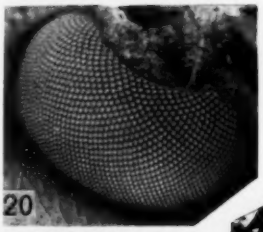
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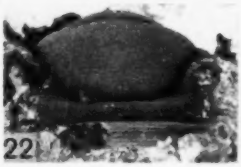
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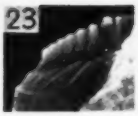
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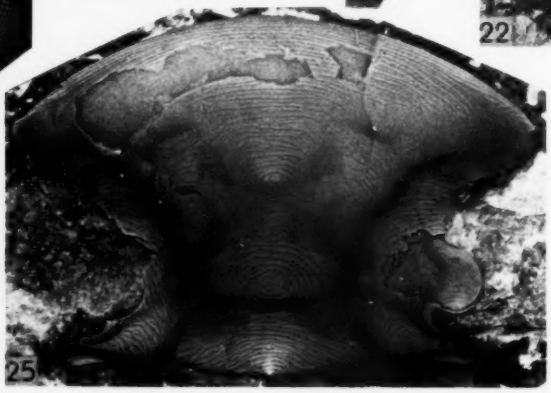
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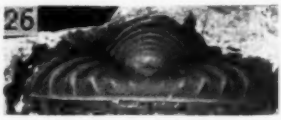
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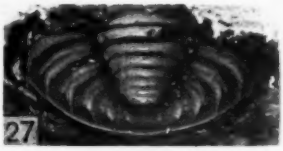
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but longitudinally by furrows which define the projecting tip. Broad pleural regions crossed by seven pairs of radially arranged grooves, ribs between these grooves gently convex, sloping more steeply posteriorly than anteriorly. Median rib between seventh pair of grooves gently convex, not subdivided. Grooves die out before reaching margin of pygidium. Doublure (pl. 54, fig. 14) broad, outer part gently convex, inner part concave and extending inward to a point about two-thirds the width of the pleural regions. External surface crossed by raised, anastomosing lines running transversely on axis and pleural regions, except close to lateral margins where they curve forward. Doublure with raised lines running subparallel to margin.

Discussion.—Genera of the Scutelluidae have recently been considered by Prantl and Přibyl (1947), Šnajdr (1958), and R. and E. Richter (in Moore, 1959). A longer work by Šnajdr is now in press. Of the fourteen genera or subgenera considered by these authors, *Scutellum* and *Bojoscutellum* seem the most likely ones to which Billings' species may be referred. The type species of *Scutellum* is *S. costatum* Pusch, 1833 (R. and E. Richter, 1926, p. 117–123, pl. 7, figs. 18–23), and American species exceedingly like it are *S. tullium* and *S. depressum* (Cooper and Cloud, 1938, p. 458–459, pl. 55, figs. 30,35–45). The Square Lake species differs from these Middle and Upper Devonian forms in the more rapidly expanding glabella, lack of preglabellar field and preglabellar furrow, presence of median glabellar tubercle, more widely divergent anterior branches of the facial suture, more prominent posteromedian projection on axis of the pygidium, and the external surface is not coarsely tuberculate. In most of these characters, however, it approaches *Bojoscutellum palifer* (Beyrich, 1845), the type species of this genus from the Lower Devonian of Bohemia (Prantl and Přibyl, 1947, pl. 1; Šnajdr, 1958, pl. 1, figs. 2,4; pl, 2, figs. 18,19). Particularly in the shape of the glabella, position and arrangement of the muscle areas, presence of median glabellar tubercle, presence and arrangement of the raised lines on the external surface, the Maine species is like *B. palifer*. It differs from it in lacking the narrow (sag. and exs.) preglabellar de-

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EXPLANATION OF PLATE 54

FIGS. *1–5*—*Mystrocephala pulchra* (Cooper and Cloud, 1938), Devonian, Calhoun County, Illinois. *1,2,4*, paratype cranidium, dorsal, left lateral, anterior views, USNM 95198c, ×6. *3*, cephalon, free cheeks displaced, exposed from ventral side, showing doublure of right free cheek, USNM 95214, ×4½. *5*, paratype pygidium, dorsal view, USNM 95198e, ×6.

6–10,12—*Mystrocephala varicella* (Hall and Clarke, 1888), Onondaga limestone, Canandaigua, New York. *6,7*, internal mould of incomplete pygidium, dorsal, left lateral views, NYSM 4225, original of Hall and Clarke, pl. 24, fig. 31, ×4. *8,12*, lectotype, internal mould and latex cast from external mould of incomplete cranidium, NYSM 4223, original of Hall and Clarke, pl. 24, figs. 29, 29a, ×6. *9,10*, internal mould of incomplete cranidium, dorsal, right lateral views, NYSM 4224, original of Hall and Clarke, pl. 24, figs. 30, 30a, ×6.

11,17–19,22,23,26,27—*Astycoryphe? junius* (Billings, 1869), Lower Devonian, Square Lake, Maine. *11*, incomplete cranidium, dorsal view, USNM 137670b, ×6. *17*, left free cheek, exterior view, USNM 137670c, ×6. *18,19,22*, incomplete cranidium, dorsal, left lateral, anterior views, USNM 137670a, ×6. *23,26,27*, pygidium, right lateral, posterior, dorsal views, USNM 137670d, ×3.

13–16,20,21,24,25—*Bojoscutellum? pompilius* (Billings, 1869), Lower Devonian, Square Lake, Maine. *13,15*, pygidium, dorsal, posterior views, USNM 137699c. ×6. *14*, pygidium, exposed from ventral side and showing doublure, USNM 137699d, ×3. *16,21,25*, cranidium, USNM 137699a; left lateral, anterior views, ×3; dorsal view, ×6. *20,24*, left free cheek, USNM 137699b; eye lobe, ×10, exterior view, ×3.

pression and in that the median rib of the pygidium is not bifurcated. In general, however, *B.? pompilius* seems to resemble *B. palifer* more than it does *S. costatum* and allied species.

Family PROETIDAE Hawle and Corda, 1847
Subfamily TROPIDOCORYPHINAE Přibyl, 1946
Genus ASTYCORYPHE R. and E. Richter, 1919
ASTYCORYPHE? JUNIUS (Billings, 1869)
Pl. 54, figs. 11,17–19,22,23,26,27

Material.—USNM 137670a–d, cranidia, free cheek, and pygidia from Lower Devonian of New Scotland limestone age, Square Lake, Aroostock County, Maine. Collected O. Nylander; P. E. Cloud, 1941.

Description.–Glabella widest across occipital ring, in front of occipital furrow narrowing progressively forward to rounded anterior lobe, lateral margins slightly pinched-in at about one-third the length; occipital furrow narrow, deep median part curved convexly forward. Two pairs of lateral glabellar furrows appear as smooth, extremely faintly indented areas, furrow 1p crescentic in outline, curving inward and backward, broader than furrow 2p which is slightly curved, inwardly and backwardly directed; furrow 3p suggested by a small area, merely an interruption in the raised lines, situated a short distance in front of the inner part of furrow 2p. Preglabellar field sloping forward, portion immediately in front of preglabellar furrow convex, forming a transverse band which continues on to the fixed cheek, anterior portion flat and sloping down to the broad, shallow, anterior border furrow. Anterior border gently convex. Eye lobe large, curved, situated close to glabella and extending from opposite the pinched-in portion back to the posterior border furrow close to extremity of occipital furrow. Anterior branch of suture straight, directed forward and slightly outward; posterior branch curving strongly outward and backward across the posterior border. Free cheek convex inside broad borders; lateral border furrow wide. posterior border furrow narrower and deeper; librigenal spine broad at base, tapering back to sharp point, border furrows continuing onto base of spine as a median depression which dies out distally. External surface bearing fine, raised anastomosing lines in Bertillon pattern, on cheek and preglabellar field running subparallel to margin. On anterior and lateral borders the lines are more prominent and run parallel to margins, similar stronger lines run along transverse ridge of preglabellar field, and on fixed and free cheeks in a curved path subparallel to the border furrow, dying out near the genal angle (pl. 54, figs. 17,18). Lines absent in furrows. Small median tubercle on occipital ring.

Pygidium with convex axis subtriangular in outline, divided into six axial rings, each ring with a slight median convexity at the posterior edge; tip of axis steeply sloping and bearing faint indication of seventh ring. Inner part of pleural regions gently sloping, narrower outer part flexed down more steeply and extending behind axis, narrow marginal rim. Four pleural furrows, anterior band of pleura convex and sloping steeply down to pleural furrow, posterior band low and sloping gently forward to pleural furrow. Four faint interpleural furrows. At the change of slope between the inner and outer of the pleural regions the anterior band of each pleura becomes narrow and sharply ridged, this narrow ridge of the first three pleural bands continuing out to the marginal rim. That of the fourth anterior pleural band does not quite reach the rim; on the change of slope between the inner and outer part of the pleural regions, ridges indicating the fifth and sixth anterior pleural bands are visible adjacent to the tip of the axis. The four posterior pleural bands extend out only as far as the change of slope in the pleural regions. External surface bearing fine, raised anastomosing lines running in curve convex forward on axial rings and along pleural bands; stronger lines on marginal rim.

Discussion.—Classification of the family Proetidae has been discussed by Přibyl (1946) and subdivisions of the genus *Proetus* by Erben (1951). Two recent arrangements of proetid genera are that by Hupé (1955, p. 200–210) and the classification by R. and E. Richter and Struve (in

Moore, 1959). The latter follows Přibyl in placing *Astycoryphe* in the subfamily Tropidocoryphinae.

With Billings (1869) I consider that the cephalon and pygidium described above belong to the same species—it is the only proetid from this locality and fairly abundant. I am indebted to Dr. H. K. Erben (personal communication) for pointing out the strong resemblance between the pygidium and that of species of *Astycoryphe* (Přibyl, 1946, p. 22–23; R. and E. Richter, 1919, p. 1–17, figures 1, 4–10). The form of the axial rings, with the backwardly projecting median tubercle, and the strong backward-curving anterior pleural bands is typical. The cephalon differs from that of typical *Astycoryphe* in that the glabella narrows less rapidly forward, the preglabellar field is shorter (sag.), and the tropidium (a narrow ridge traversing the preglabellar field and the cheek a short distance inside the border furrow) is not typically developed. However, the transverse ridge in *A? junius* that runs immediately in front of the preglabellar furrow and is continued by an extremely faint ridge, marked by strong lines on the external surface, curving across the cheek just outside the eye lobe (pl. 54, figs. 11,17,18), may represent the tropidium in process of development. Thus the species from Maine has been referred with question to *Astycoryphe*, and if it does belong to this genus it is the oldest species in it. *A. gracilis* (Barrande, 1846) occurs in the Lower Devonian of Bohemia, in beds that range to the upper limit of the Lower Emsian, though the exact horizon at which the species occurs is not well known (H. K. Erben, personal communication). Dr. Erben also reports that in Germany he has found *A. gracilis* in limestones of Upper Emsian age.

A? junius displays some similarity to species of *Proetus* (*Cornuproetus*) described by Erben (1951, p. 25–30, figs. 5,6). Though the glabella of *A? junius* shows the slight pinching-in at one-third the length, the glabella in front of this constriction contracts more rapidly forward than in the species described by Erben. In addition *Proetus* (*Cornuproetus*) has a short (sag.) preglabellar field which slopes forward and lacks the convex ridge visible in *A? junius*. Because of these differences therefore I prefer to place the Maine species in *Astycoryphe* with question.

REFERENCES

AMSDEN, T. W., 1956a, Catalogue of Hunton fossils: Oklahoma Geol. Surv., Circular 38, 63 p.

——, 1956b, Additional fossils from the Hunton group, Oklahoma: Oklahoma Geol. Surv., Okla. Geol. notes, v. 16, no. 12, p. 138–139.

BILLINGS, E., 1869, Description of some new species of fossils with remarks on others already known, from the Silurian and Devonian rocks of Maine: Proc. Portland Soc. Natur. Hist., v. 1, pt. 2, p. 104–126, fig. 1–28.

CLARKE, J. M., 1892, On *Cordania*, a proposed new genus of trilobites: N. Y. State Mus., 45th Ann. Rep. for 1891, p. 440–443.

——, 1900, The Oriskany fauna of Becraft Mountain, Columbia County, N. Y.: Mem. N. Y. State Mus., no. 3, v. 3, 128 p., pls. 1–9.

——, 1908, Early Devonic history of New York and eastern North America: N. Y. State Mus., Mem. 9, 366 p., 48 pls.

COOPER, G. ARTHUR, *et al.*, 1942, Correlation of the Devonian sedimentary formations of North America: Bull. Geol. Soc. America, v. 53, p. 1729–1794, 1 pl.

——, & CLOUD, P. E., 1938, New Devonian fossils from Calhoun County, Illinois: Jour. Paleontology, v. 12, p. 444–460, pls. 54,55.

ERBEN, H. K., 1951, Beitrag zur Gliederung der Gattung *Proetus* Stein., 1831 (Trilobitae): Neues Jb. Geol. u. Paläontol., Abh., v. 94, p. 5–48, pls. 2–4, 12 figs.

GOLDRING, R., 1955, The Upper Devonian and Lower Carboniferous Trilobites of the Pilton Beds in N. Devon: Senckenberg. lethea, v. 36, p. 27–48, pls. 1,2; 7 figs.

——, & STUBBLEFIELD, C. J., 1957, *Brachymetopus* (*Brachymetopus*) and *B.* (*Brachymetopina*) (Trilobita, Devonian to Upper Carboniferous): Geol. Mag., v. 94, p. 421–424.

HALL, J., & CLARKE, J. M., 1888, Trilobites and Other Crustacea: Nat. Hist. New York, Paleontology, v. 7, Supp. to v. 5, part 2, 236+42 p., pls. 1–36+114–129.

HUPÉ, P., 1953, Classe des Trilobites *in* Traité de Paléontologie, v. 3, p. 44–246, Ed. J. Piveteau. Paris.

——, 1954–5, Classification des Trilobites: Ann. Paleontol., v. 39, p. 1–110, 92 figs.; v. 41, p. 111–345, figs. 93–247.

KILFOYLE, C. F., 1954, Catalogue of type specimens of fossils in the New York State Museum, suppl. 4; N. Y. State Mus., Bull. 348, 719 p.

MAKSIMOVA, Z. A., 1957, On the morphology of the genus *Brachymetopus* M'Coy: Ann. All-Union Pal. Soc., v. 16, p. 58–63, 1 pl. (in Russian).

MITCHELL, J., 1922, Description of Two New Trilobites, and Note on *Griffithides convexi-*

caudatus Mitchell: Proc. Linnaean Soc. New South Wales, v. 47, p. 535–540, pl. 54.

MOORE, R. C. (Editor), 1959, Treatise on Invertebrate Paleontology, Part O, Arthropoda 1: Geol. Soc. America and Univ. Kansas Press, 560 p., 415 figs.

PŘANTL, F., & PŘIBYL, A., 1947, Classification and Division of the genus *Scutellum* Pusch, 1833, from the Barrandian (central Bohemia): Bull. Int. l'Acad. tchèque Sci., v. 47, no. 9, 32 p., 7 pls.

——, 1951, A revision of the Bohemian Representatives of the Family Otarionidae R. and E. Richter (Trilobitae): Stát. Geol. Úst. Československ. Repub., v. 17 (for 1950), p. 353–512 (Czech and English text, Russian summary), 5 pls.

PŘIBYL, A., 1946, Notes on the Recognition of the Bohemian Proetidae (Trilobitae): Bull. Int. l'Acad. tchèque Sci., v. 46, 41 p., 4 pls.

RICHTER, R., & RICHTER, E., 1919. Der Proetiden—Zweig *Astycoryphe-Tropidocoryphe-Pteroparia:* Senckenbergiana, v. 1, p. 1–17, 25–51, 18 figs.

——, 1926, Die Trilobiten des Oberdevons, 4: Abh. Preuss. Geol. Landes., N. S., v. 99, 314 p., 12 pls.

——, 1954, Die Trilobiten des Ebbe-Sattels: Abh. Senckenb. Naturf. Ges., v. 488, p. 1–76, 6 pls.

——, 1955, Scutelluidae n.n. (Tril.): Senckenberg. lethea, v. 36, p. 291–293.

SCHMIDT, H., 1958, Zur Frage des Genotypus von *Brachymetopus* M'Coy: Senckenberg. lethea, v. 39, p. 153–156.

SINCLAIR, G. W., 1946, The Ordovician Trilobite *Dimeropyge*; Am. Jour. Sci., v. 244, p. 854–860, pl. 1.

ŠNAJDR, M., 1958, Some New Genera of Trilobites of the Family Scutelluidae; Věstník ÚÚG, v. 33, p. 177–184, pl. 1,2 (Czech text, English summary).

STUMM, E. C., 1953, Trilobites of the Devonian Traverse Group of Michigan: Contrib. Mus. Paleont., Univ. Michigan, v. 10, no. 6, p. 101–157, 12 pls.

TSCHERNYSCHEW, T., 1893, Die Fauna des unteren Devon am Ostabhange des Ural: Mém. Comité Géol., St. Pétersbourg, v. 4, no. 3, 221 p., 14 pls.

WHITTINGTON, H. B., 1957, The Ontogeny of Trilobites: Biol. Rev., Cambridge, v. 32, p. 421–469, 29 figs.

WOODWARD, H., 1883–1884, A Monograph of the British Carboniferous Trilobites: Palaeontographical Soc., London, 86 p., 10 pls.

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HYPOTYPES OF *PHYLLOCERAS ONOENSE* STANTON

E. L. PACKARD
Stanford University, Stanford, California

ABSTRACT—A lectotype of *Phylloceras onoense* Stanton, the type species of the genus *Hypophylloceras*, is here selected from the two original specimens of *Ammonites ramosus* Gabb (not Meek) on which Stanton (in part) originally based his species. Gabb's two specimens are not conspecific, and a possible new species of *Hypophylloceras* is suggested for the second specimen.

INTRODUCTION

BECAUSE *Phylloceras onoense* Stanton 1896 (1895), the type species of the genus *Hypophylloceras* Salfeld, 1924, was never adequately described or figured, the specimens of *Ammonites ramosus* Gabb (1864), (not Meek) on which Stanton (in part) based his species, are herein redescribed and figured, along with other significant specimens which contribute to the understanding of this species. Gabb's specimens are in the Museum of Paleontology, University of California, Berkeley; the other figured specimens are in the collections of the Academy of Natural Sciences of Philadelphia and the U. S. Geological Survey and the U. S. National Museum.

HISTORY OF THE SPECIES

Gabb (1864, p. 65, pl. 11, figs. 12, 12a; pl. 12, fig. 12b) reported the occurrence of two imperfect specimens of phylloceratids from the "lower division of the California Cretaceous at Cottonwood Creek, Shasta County," which he referred to *Ammonites ramosus* Meek of Late Cretaceous age. Stanton (1896, p. 72–75) recognized that Gabb's identification was incorrect, and proposed the name *Phylloceras onoense* [*recte onoensis*] for these specimens, as well as for others in his own collection from the neighborhood of Ono on Cottonwood Creek.

Merriam (1895, p. 1) reported that Gabb's original specimens are in the collections of the University of California. However, Anderson (1938, p. 142) failed to recognize them and erroneously proposed as a lectotype of *P. onoense* a specimen from the "West branch of Bee Creek" in the Cottonwood district (Cal. Acad. Sci. Loc. 1347). A recent search of the collections at Berkeley, aided by Joseph Peck, has brought to light Gabb's original specimens. One of these (Univ. Calif. Mus. Pal. No. 12110) is here selected as the lectotype of *Phylloceras onoense* Stanton.

Three other specimens identified as *Ammonites ramosus* by Gabb were examined through the courtesy of Horace G. Richards, Academy of Natural Sciences of Philadelphia. It is not known when Gabb collected these specimens, but it probably was subsequent to 1869 as only two specimens are mentioned in his publication of that date (p. 210). These specimens are described herein.

Stanton (1896, p. 74) proposed the specific name *onoensis* in connection with his description of *Phylloceras knoxvillenis*. He mentioned having collected several specimens of the former species from "near the original locality in the neighborhood of Ono." Those specimens could not be found by the late J. B. Reeside, Jr. in either the U. S. National Museum or the U. S. Geological Survey collections. However, Reeside did discover one specimen of *P. onoense* collected by Stanton from U.S.G.S. Mesozoic locality 2246 (Albrights ranch near Roaring River, four miles south of Ono). A cast of this specimen is figured on plate 56, figure 1. More recently David Jones discovered in the Upper Cretaceous collections of the U. S. National Museum collections (no. 21520) a specimen obtained by Diller and Brown in 1889 and subsequently identified by Stanton as *P. onoense*. The label states that it was from Aldersons Gulch, 1½ miles southeast of Ono. It is briefly described and illustrated below.

ACKNOWLEDGMENTS

Appreciation and thanks are here expressed to Dr. S. W. Muller for his personal interest and help in this study. The writer is grateful for the valuable discussions with him, Dr. Hubert Schenck and Dr. Tatsuro Matsumoto. Dr. Muller and Dr. Matsumoto drew several of the suture lines. The writer is also grateful to Dr. H. G. Richards for the loan of specimens labeled by Gabb now in the Academy of Natural History of Philadelphia. The late Dr. J. B. Reeside searched the collections of the U. S. Geological Survey for Stanton's types. Specimens in the University of California at Berkeley were made available for study by Dr. J. Wyatt Durham and Mr. Joseph H. Peck. Dr. Leo Hertlein assisted in the study of the several specimens in the California Academy of Sciences. The field occurrences of this species were clarified by Dr. M. A. Murphy, University of California, Riverside. Dr. David Jones has critically read the manuscript.

SYSTEMATIC DESCRIPTIONS

Class CEPHALOPODA
Family PHYLLOCERATIDAE Zittel 1884
Subfamily PHYLLOCERATINAE Zittel 1884
Genus HYPOPHYLLOCERAS Salfeld 1924

Type species.—*Phylloceras onoense* Stanton 1896 [1895]

HYPOPHYLLOCERAS ONOENSE (Stanton)
Pl. 55, figs. 1–4; pl. 56, fig. 1

Ammonites ramosus Gabb (not Meek, 1857, 1876) (in part), 1864, p. 65, pl. 12, fig. 12b.
Phylloceras onoensis Stanton, 1896 (1895), p. 74.
Phylloceras onoense Smith, 1898, p. 147–149, pls. 19,20; Anderson, 1938, p. 142, pl. 11, figs. 1,2; Hanna & Hertlein, 1943, p. 68, fig. 19.
Hypophylloceras onoense Salfeld, 1924, p. 6; Spath, 1927, p. 38; Collignon, 1949, p. 68 (in part); Wright (in Arkell *et al.*), 1957, p. L189, fig. 219; Murphy, 1956, fig. 6.

The two specimens of *Ammonites ramosus* Gabb (not Meek) (Univ. Calif. Mus. Pal. Nos. 12109 and 12110) are the only known syntypes of *Phylloceras onoense* Stanton from which to select a lectotype of this species. The specimen (U.C.M.P. No. 12109) figured by Gabb (pl. 11, fig. 12) is not conspecific with the other specimen from which the suture shown on his plate 12, figure 126 was obviously drawn.

That specimen (U.C.M.P. No. 12110) is here considered to be specifically identical to two known specimens identified by Stanton and also to Anderson's illegally designated "lectotype." The latter has been cited as the type of *P. onoense* (Wright, 1957, p. L189).

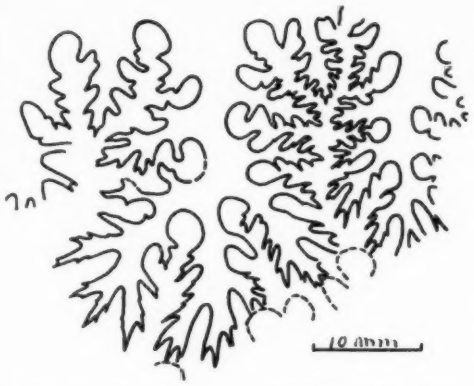
Description.—The proposed lectotype (U.C.M.P. No. 12110) consists of less than one-half of a septate whorl. The specimen has been partially crushed and lacks the outer shell layer on parts of both sides. The several imperfectly preserved sutures must have been the basis for Gabb's illustration.

The shell is compressed, with a whorl height of about 56 percent of the estimated diameter. Whorl section is a flattened ellipse with a ratio of width to height of about .54. Greatest width is a little dorsal of the mid flank. Flanks are slightly convex, sloping to the relatively narrow and evenly arched venter. Umbilicus is small, deep, equalling in diameter approximately 14 percent of the whorl height. Its wall curves gently and evenly onto the flank without any shoulder demarkation.

Ornamentation consists of very fine riblets or lirae. At the umbilicus they appear as little more than crowded growth lines that trend slightly forward. They are not observable, probably due to the poor preservation, on the inner flank region. Farther out the riblets seem to be nearly radial and cross the venter with a very slight forward curve. These riblets are very fine being hardly visible without magnification. They have rounded cross sections and interspaces a little wider than the riblets. Thirteen ribs were counted near the venter within the length of one centimeter, at the whorl height of 70 millimeters.

A number of incomplete sutures, somewhat simplified by erosion, are exposed on the left side of the lectotype and a well preserved first lateral lobe and parts of the adjacent saddles on the right side. These sutures, as drawn by Matsumoto, are shown as text-figures 1 and 2.

The ventral lobe and part of the first saddle are not preserved. The first lateral

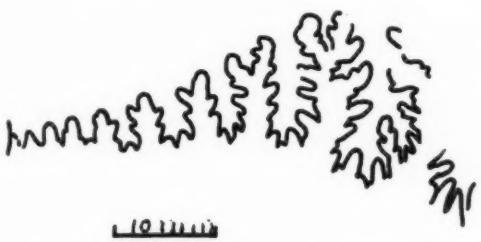


TEXT-FIG. *1*—Suture line of lectotype of *Hypophylloceras onoense* (Stanton) U.S.M.P. no. 12110. The first lateral lobe and adjacent saddles at whorl height of about 60 mm. On right side of whorl. Enlarged.

lobe is narrow, deep and unsymmetrically trifid, with the inner inflection largest and most complex. Two oblique elements separate the three divisions and are themselves incised and terminate in phylloid ends. The second lateral lobe, as shown on the right side, is narrow, not as deep as the first lobe and very unequally bifid, with the inner inflection very much larger and deeper. The first four auxiliary lobes become increasingly narrow and less distinctly incised. The last four lobes are very narrow and are essentially without recognizable inflections.

The first lateral saddle, on the right side, is complete except for its outermost lower element. It is narrow, high and deeply symmetrically bifid. Both branches are further divided with conspicuous phylloid terminations. The main lateral inner inflection is deep and oblique to the axis of the saddle.

The second saddle has about the same height as the first. It is bifid with the outer branch deeply and obliquely incised, terminations are phylloid. The saddles on the left side probably were a little more complex than shown in text-figure 2. The second saddle on the left side is narrow, high and shallowly divided with but few lateral inflections. Auxiliaries become progressively lower and narrower; the last few are only indistinctly inflected.



TEXT-FIG. *2*—Suture line of lectotype as exposed on the left side at whorl height of about 55 mm. Some details lost by erosion.

Measurements of the lectotype of Hypophylloceras onoense (Stanton) (in millimeters)

Estimated diameter of the septate specimen	125
Height of last whorl	70±
Thickness of last whorl	38±
Diameter of umbilicus	10

The lectotype differs specifically from Gabb's other original specimen (U.C.M.P. No. 12109). It is more compressed, has flatter flanks, a narrower periphery, and more numerous and finer ribs.

Stanton's identified specimen.—The specimen collected and identified by Stanton in 1900 (U. S. Geol. Surv. Loc. 2246) supplements the description of the lectotype of *Hypophylloceras onoense*. This description is based upon a plaster cast of that specimen which is herein illustrated on plate 2, figure 1. It is well preserved undeformed, septate, with a diameter of 114 millimeters. It is compressed and has a whorl height greater than its width. Greatest thickness is just below mid flank. The wall of the small umbilicus slopes regularly onto the slightly convex flank. Venter is narrowly rounded. Ornamentation consists of numerous fine riblets with wider interspaces which apparently conform in direction to the faint slightly sigmoidal growth lines.

Measurements of Stanton's identified specimen (in millimeters)

Maximum diameter	114
Height of last whorl	77
Thickness	33
Diameter of umbilicus	9±
Height of preceding whorl	29

This specimen resembles the lectotype of

H. onoense in its general proportions, including the flattened flank, narrow periphery and character of its ribbing. The ribs show some evidence of a slight double curvature on the flank not shown on Gabb's specimen. Sutures of the two are similar.

A second specimen identified by Stanton.—This specimen (U.S.N.M. No. 21520) from Alderson's Gulch near Ono may have been one of Stanton's syntypes of *P. onoense* since it was obtained by Diller in 1889. It is compressed with a narrow venter numerous fine ribs and well preserved sutures, all of which characters agree closely with the lectotype.

Measurements of second specimen identified by Stanton (in millimeters)

Maximum diameter	165±
Height of last whorl	90±
Height of preceding whorl	42
Thickness	48+
Diameter of umbilicus	10

Anderson's "lectotype."—The specimen incorrectly designated by Anderson as a "lectotype" (type No. 7336, Calif. Acad. Sci.) is wholly septate with a diameter of 120 millimeters. It agrees with the proposed lectotype in its narrow periphery, somewhat flattened flanks, ribbing and in sutural elements. Anderson's figure of the suture (1938, pl. 11, fig. 1) has been incorrectly retouched as regards the first saddle.

Murphy recently has studied Anderson's "lectotype" and specimens of the same species in his personal collection. He (letter, July, 1938) has noted very fine, transverse ribbing at a diameter of 13 millimeters, and sigmoidal constrictions on the internal cast at 4 millimeters. The latter continue to occur up to a diameter of approximately 45 millimeters.

Measurements of Anderson's specimen (in millimeters)

Maximum diameter	120
Height in last whorl	65
Thickness	35
Diameter of umbilicus	7

Type locality and occurrences.—The type locality of the lectotype of *H. onoense* is indefinite. Gabb reported his two specimens from Cottonwood Creek, Shasta County, California. The specimen (U.S.G.S. No. 2246) identified and collected by Stanton, herein considered specifically identical with the lectotype, came from Albrights ranch near Roaring River, about four miles south of Ono (U.S.G.S. Loc. 2246). The second specimen (U.S.N.M. No. 21520) identified by Stanton came from Aldersons Gulch, one and one-half miles southeast of Ono. Anderson's "lectotype" was reported in his text (p. 143) from "the West Branch of Bee Creek half a mile east of Shoup ranch house in the Argonaut zone." However, the same specimen was cited in the explanation of plate 11 from locality number 1347 (C.A.S.) which according to the Academy's Locality Book is north of Roaring River five miles south of Ono on the road to Milsap's, north of Barr's Corral.

Age.—The stratigraphic range of this

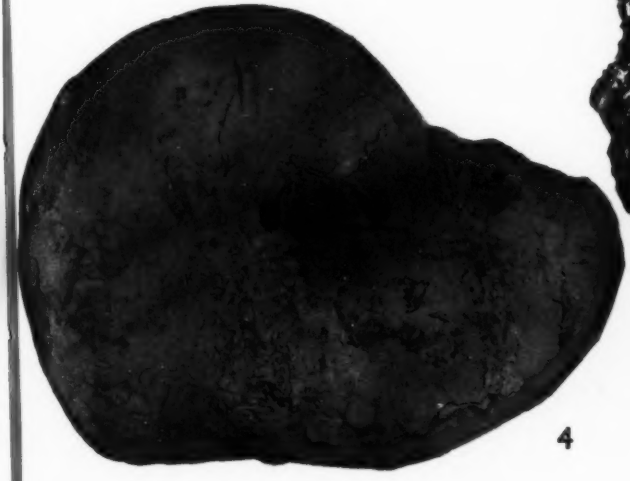
EXPLANATION OF PLATE 55

FIGS. *1–4—Hypophylloceras onoense* (Stanton). *1,2*, lateral views of lectotype (no. 12110, Univ. Calif., Mus. Paleo.) This is Gabb's hypotype of *Ammonites ramosus* Meek and a syntype of *Phylloceras onoense* Stanton, ×1; *3*, ventral, *4*, lateral views of a referred specimen identified by Stanton (no. 21520 U.S.N.M.) ×½.

1

3

2



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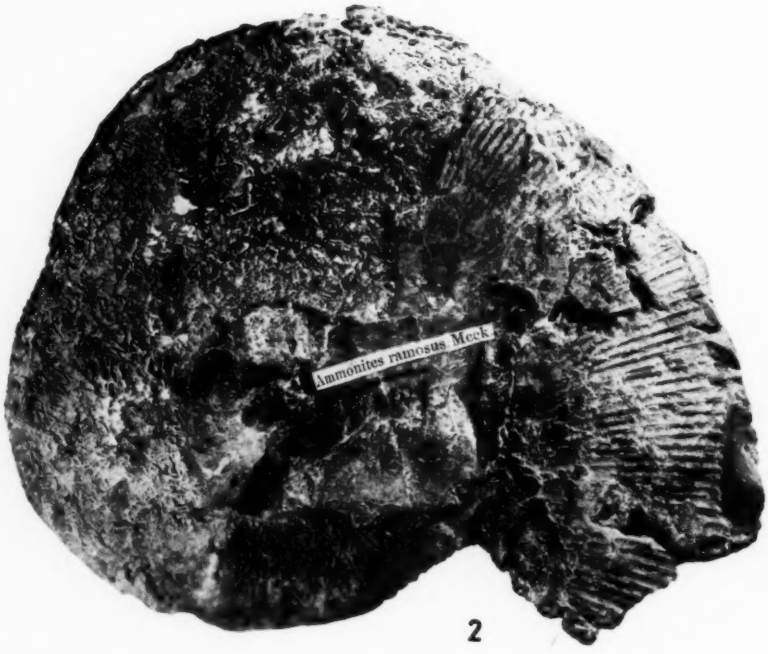


2

species in the Lower Cretaceous rocks of northern California is at present uncertain. Anderson reported his specimen from his Argonaut zone which is included in Murphy's (1956) *Gabbioceras wintunium* zone of early Aptian age.

HYPOPHYLLOCERAS n. sp?
Pl. 56, fig. 2; pl. 57, figs. 1–3

Ammonites ramosus Gabb, 1864 (in part), p. 65, pl. 11, figs. 12,12A?

Description.—This specimen (U.C.M.P. No. 12109) consists of a deeply septate whorl on which diagnostic characters are confined to the anterior third of one side. Maximum diameter was not less than 135 millimeters. Whorl section is higher than wide, height equalling about 66 percent of the diameter. Greatest thickness is near the middle of the flank, umbilicus is small and rounds evenly to the convex flank. Venter is broadly and evenly arched. Ornamentation near the umbilicus consists of fine striae which become more prominent on the mid flank and increase in strength toward the venter where they cross with a very slight forward curve. Ribs are sharply crested near the venter with interspaces a little wider than the ribs. Five or six ribs per centimeter are present near the periphery at the anterior end and at the diameter of 116 millimeters. No evidence is seen for a backward curving of the ribs as shown on Gabb's figure.

One side of this specimen shows traces of several incomplete sutures which have been deeply weathered and show only a few phylloid terminations.

Measurements of specimen (U.C.M.P. No. 12109) (in millimeters)

Maximum diameter (estimated)	135
Height of last whorl	80
Maximum thickness of last whorl	46±
Diameter of umbilicus	10
Height of preceding whorl	37

This specimen differs from the lectotype of *H. onoense* in its greater convexity of flanks, broader venter and much coarser ribbing.

Specimen identified by Gabb as ramosus *subsequent to 1864.*—Three specimens now in the paleontological collections of the Academy of Natural Sciences of Philadelphia (No. 12885) were labeled *Ammonites ramosus* by Gabb some time subsequent to 1864. The largest of these has a whorl height equal to about 60 percent of the diameter. Umbilicus small without distinct shoulders. Greatest thickness a little below middle of the convex flank. Venter broadly rounded. Details of ribbing obscure but rather coarse. Suture line of this specimen as drawn by Muller is reproduced on plate 57, fig. 3, taken at a whorl height of 58 millimeters.

Measurements of the largest of the specimens in the Academy at Philadelphia (No. 12885) (in millimeters)

Maximum diameter	118
Height of last whorl	71
Thickness	36±
Diameter of umbilicus	9±
Height of preceding whrol	29

EXPLANATION OF PLATE 56

FIG. 1—*Hypophylloceras onoense* (Stanton). Cast of a referred specimen collected and identified by Stanton in 1900. From Stanton's locality number 2246 U.S.G.S. This plaster cast has been cut for a cross section; ×1.

2—*Hypophylloceras* (n.sp.?) Lateral view of Gabb's figured hypotype of *Ammonites ramosus* Meek, no. 12109, U.C.M.P. Both approximately natural size.

TABLE 1—SUMMARY OF DIMENSIONS

	Maximum Diameter		Height of of Last Whorl		Thickness of Last Whorl		Diameter of Umbilicus		Height preceding Whorl	
	mm.	%	mm.	%	mm.	%	mm.	%	mm.	%
Ammonites ramosus Meek (plastoholotype, 2451, U.S.G.S.)	48.2	100	28	.58	113	.27	3	.6	9.6	.19
Ammonites ramosus Gabb (lectotype *H. onoense* Stanton, U.C.M.P. 12110)	125±	100	70±	.56	38±	.30	10	.8	—	—
Phylloceras onoense (identified by Stanton, 2246, U.S.G.S.)	114	100	77	.67	33	.21	9±	.7	29	.25?
Phylloceras onoense (identified by Stanton, 12520, U.S.N.M.)	165±	100	90±	.54	48±	.29	10	.57	42	.25
Phylloceras onoense (Anderson's lectotype 7336 C.A.S.)	120	100	65	.54	35	.29	7	.5	—	—
Hypophylloceras, n. sp.? (Gabb's specimen, 12109 U.C.M.P.)	135±	—	80±	—	46	—	10	—	37	—
Hypophylloceras, n. sp.? (12885 Acad. Nat. Sci. Phila.)	118	100	71	.60	36±	.30	9±	.7	38	.31

The other two specimens in that Philadelphia Academy collection labeled by Gabb are smaller and appear to represent immature individuals of the same species.

It is considered probable that this large well preserved specimen (No. 12885, Acad. Nat. Sci. Phil.) is specifically identical with the specimen figured by Gabb (1864, pl. 11, fig. 12). Both have about the same proportions, convexity of their flanks, rather broadly rounded venters and similar ribbing. They do not appear to represent any of the several species first described from the Pacific Coast of North America.

Although Gabb's specimen (U.C.M.P. No. 12909) and possibly those in the Academy of Natural Sciences of Philadelphia may represent a new species of *Hypophylloceras* it does not appear advisable to propose a name since the original collecting locality is very indefinite.

The dimensions of these several specimens described above and those of the plastoholotype of *Ammonites ramosus* Meek (not Gabb) are summarized in table I for direct comparisons.

Stanton (1896, p. 74) correctly recognized that his species was distinct from the Upper Cretaceous species, *Ammonites ramosus* Meek, which has since become the type of *Neophylloceras* Shimizu (1934). That author and later Wright and Matsumoto (1956, p. 109) discussed Meek's species and compared it with Japanese forms including *Neophylloceras subramosum* Shimizu (1934). They maintained that *Neophylloceras* is a valid genus, distinguished from *Hypophylloceras* by the reduction of the phylloid terminations of the saddles, among other lesser characters. This writer concurs with them, and accepts their generic distinctions.

LITERATURE CITED

ARKELL, W. J., KUMMEL, BERNARD & WRIGHT, C. W., 1957, Mesozoic Ammonoidea: Treatise of Paleontology, p. L80-440, figs. 124–558.

COLLIGNON, MAURICE, 1949, Faune Neocomienne des couches a Crioceres de Belohasifaka (Cercle de Sitampiky) (Madagascar): Ann. Geol. Serv. Mines, Madagascar, fasc., 15, p. 55–83, pls. 8 (1)–13 (6), 8 text figs.

GABB, W. M., 1864, Descriptions of Cretaceous fossils: Geol. Surv. California, Paleont., v. 1, p. 58–81, 102–236 (in part), pls. 9-31.

——, 1869, Cretaceous fossils—descriptions of a

new species (California): Geol. Surv. California, Paleont., v. 2, p. 127–254 (in part), pls. 19–34.

HANNA, G. D. & HERTLEIN, L. G., 1943, Characteristic fossils of California: Calif. Dept. Nat. Res., Div. Mines, Bull. 118, Chapt. 6, p. 165–185, figs. 60–71.

KOSSMAT, FRANZ, 1895–1898, Untersuchungen über die südindischen Kreideformation: Beitr. Paleont. Geol. Oest-Ung., IX (1895), p. 97–203, pls. 15–25.

MICHELIN, HARDOUIN, 1833–1834, Magasin de Zoologie, de Guerin (1833), pl. 35.

MURPHY, M. A., 1956, Lower Cretaceous stratigraphy units of northern California: Bull. Am. Assoc. Petroleum Geologists, v. 40, no. 9, p. 2098–2119, 6 figs.

MEEK, F. G., 1857, Descriptions of new organic remains from the Cretaceous of Vancouver's Island: Trans. Albany Inst., v. 4, p. 33–49 (1858–64).

——, 1876, Descriptions and illustrations of fossils from Vancouver's and Sucia Islands, and other northwestern localities: Bull. U. S. Geol. and Geogr. Surv. Terr., v. 2, p. 350–374, pls. 1–6.

MERRIAM, J. C., 1895, List of types in the Geological Museum of the University of California: 3 p., Geology Dept., Univ. California, Berkeley.

PERVINQUIERE, L., 1907, Etudes de Paleontologie Tunisienne, I, Cephalopodis des Terrains secondaires, 438 p., 158 text-figs., Atlas, 27 pls.

SALFELD, HANS, 1924, Die Bedeutung der Konservatirstämme für Stammesent wicklung der Ammonoiden: 16 p., 57 figs., 16 pls. (Leipzig) Max Weg.

SHIMIZU, SABURI & OBLATA, T., 1934, Cephalopoda in Iwanami's Lecture Series of Geology—Paleontology: 137 p. Tokyo [in Japanese].

——, 1935, The Upper Cretaceous cephalopods of Japan: Pt. I: Jour. Shanghai Sci. Inst. sec. 2, v. 1, p. 159–226, text figs. 1–5, tables.

SMITH, J. P., 1898, The development of *Lytoceras* and *Phylloceras*: Proc. Calif. Acad. Sci., (3), v. 1, no. 4, p. 129–156, pls. 16–19.

SPATH, L. F., 1927, Revision of the Jurassic cephalopod fauna of Kacch (Cutch): Mem. Geol. Surv. India, n. ser., v. 9, mem. 2, pt I, p. 1–71, pls. 1–7.

STANTON, T. W., 1896 (1895), Contributions to the Cretaceous paleontology of the Pacific Coast. The fauna of the Knoxville beds: U. S. Geol. Surv. Bull. 133, 132 p., 2 pls.

STOLICZKA, F., 1861–1865, The fossil cephalopods of the Cretaceous rocks of southern India, Ammonoidea: Pal. Indica, ser. 1, v. 1, p. 41–216, appd. p. 1–9, 94 pls.

WHITEAVES, J. F., 1900, On some additional or imperfectly understood fossils from the Cretaceous rocks of the Queen Charlotte Islands, etc.: Geol. Surv. Canada, Mesozoic Fossils, v. 1, pt. 4, p. 263–305, pls. 33–39.

WRIGHT, C. W., & MATSUMOTO, TATSURO, 1954, Some doubtful Cretaceous ammonite genera from Japan and Saghalien: Mem. Faculty of Sci., Kyushu Univ., ser. D, v. 4, no. 2, p. 107–134, pls. 7–8.

WRIGHT, C. W., 1957, *in* ARKELL, W. J., KUMMEL, BERNARD, & WRIGHT, C. W., Mesozoic Ammonoidea: Treatise on Invertebrate Paleontology (L) Mollusca 4, Geol. Soc. America and University Kansas Press.

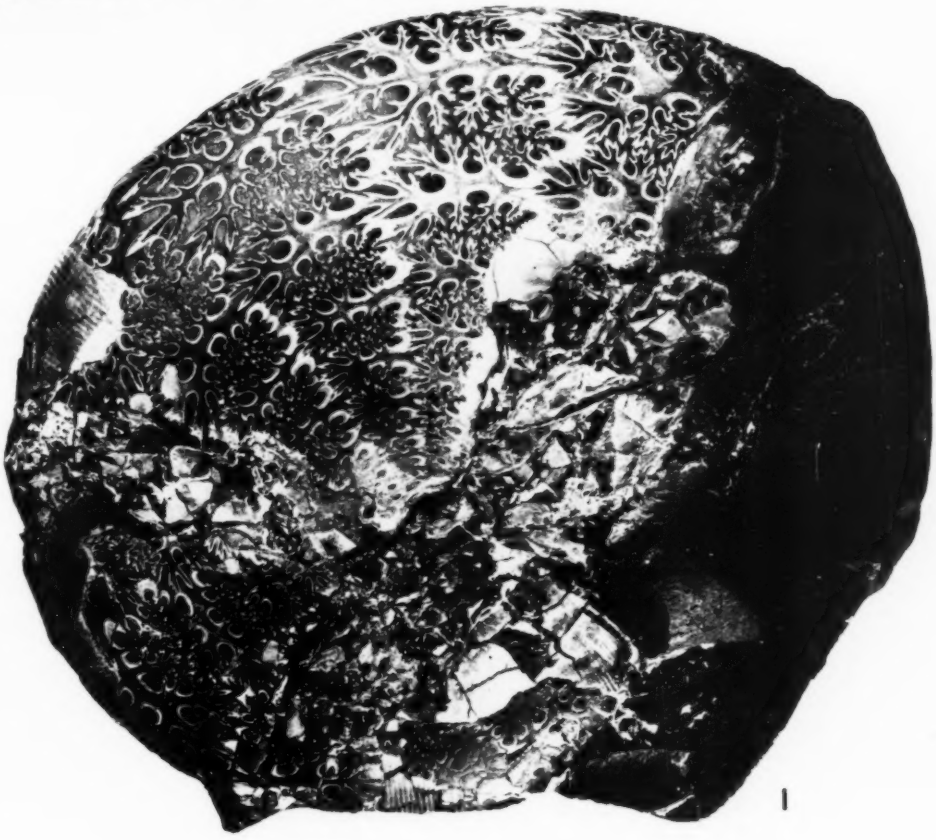
ZITTEL, K. A. VON, 1884, Handbuch des Palaeontology, Abt. 1, Bd. 2, 893 p., 1109 fig. (Cephalopods, p. 329–522).

MANUSCRIPT RECEIVED MAY 5, 1959.

(*Explanation of* PLATE 57 *on next page*)

EXPLANATION OF PLATE 57

FIGS. *1–3*—Hypophylloceras n.sp.? *1,2*, Lateral and ventral views of a specimen identified by Gabb, subsequent to 1864, as *Ammonites ramosus* Meek (no. 12885 Acad. Nat. Hist. Philadelphia), ×1. *3*, Suture line of same specimen.



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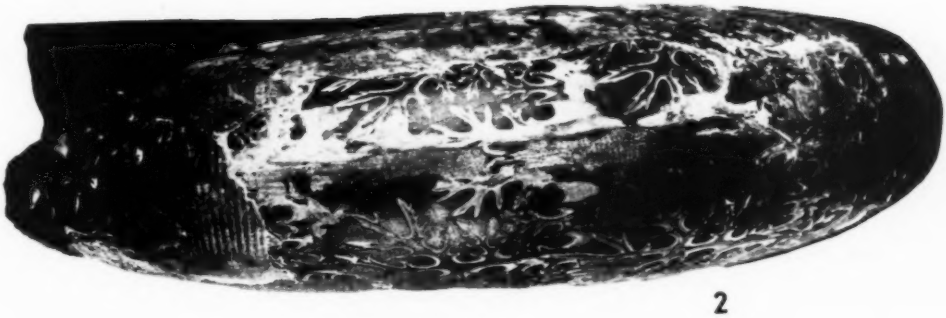

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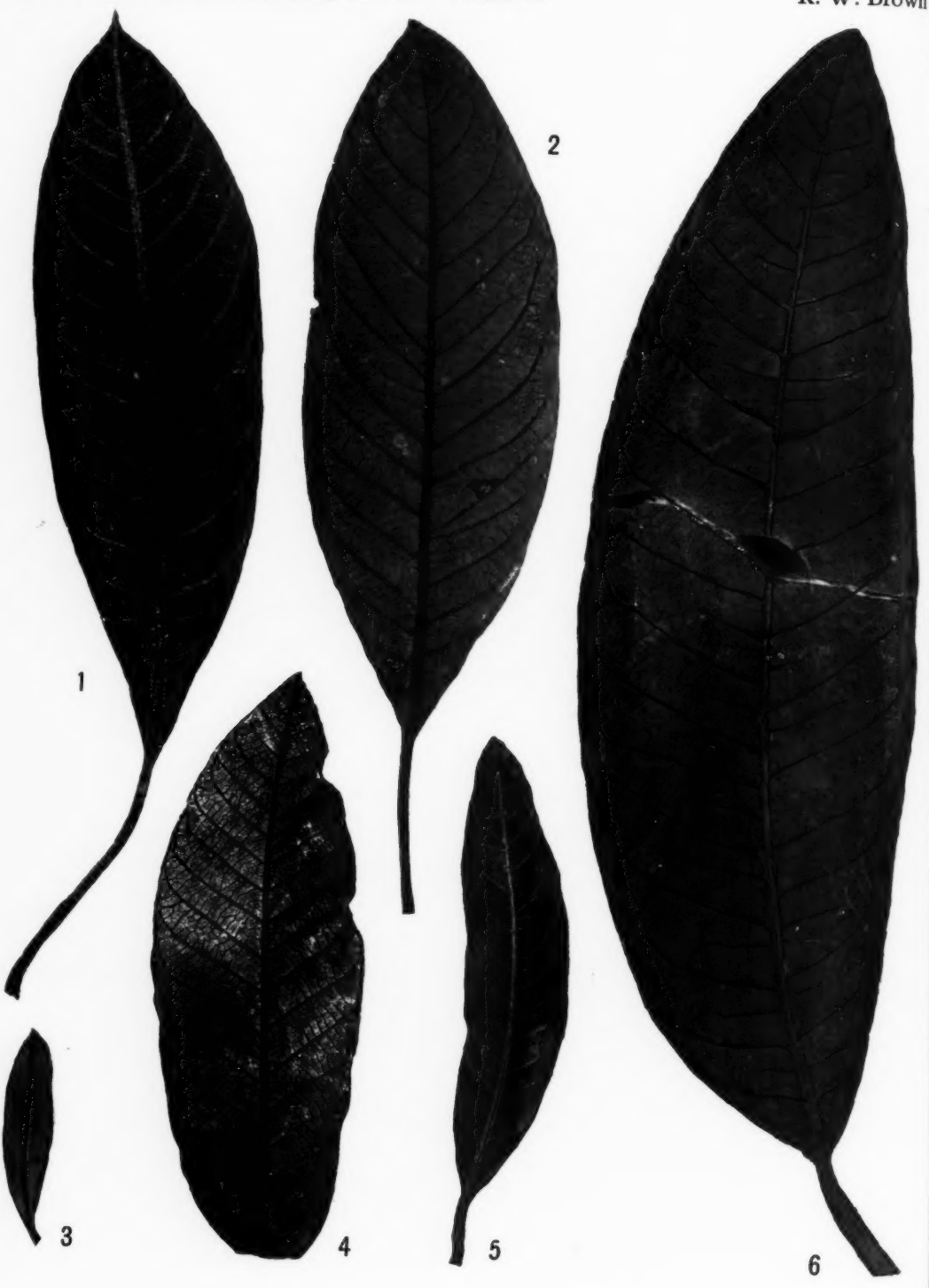
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JOURNAL OF PALEONTOLOGY, V. 34, NO. 3, P. 429–432, PL. 58, MAY, 1960

CORKWOOD IN THE EOCENE FLORA OF THE SOUTHEASTERN UNITED STATES

ROLAND W. BROWN[1]
Lehighton, R.F.D. 3, Pa.

ABSTRACT—Eight species in seven genera, none heretofore identified as *Leitneria* (corkwood), are synonymized as *Leitneria eocenica* (Berry) Brown, n. comb., the first recognition of that genus in the Eocene flora of the southeastern United States. This example points the need for a thorough restudy of the entire flora.

INTRODUCTION

ON PAGE 73 of *The lower Eocene floras of southeastern North America*, 1916, the late E. W. Berry stated in general terms his method of studying collections of fossil plants. In essence this consisted first of comparing the fossils with the corresponding parts of similar or identical species now living in or near the same region; second, failing to find satisfactory matches, to look into exotic floras; and third, to gather what suggestions can be had from paleobotanical literature but with not too much reliance on the latter for dependable help. That he was not too successful in applying the method will be seen from his treatment of the specimens I here refer to corkwood (*Leitneria*), and from numerous other misidentifications, some of which are discussed to emphasize the need for a complete restudy of the Eocene floras of the Gulf coastal area.

[1] Retired from the U. S. Geological Survey, Dec. 31, 1958.

The application of Berry's method implies on the part of the practitioner a fairly thorough knowledge of the morphology, classification, geographic distribution, and environmental circumstances of living plants. Not the least of these is morphology, particularly the gross and subtle features that permit distinction and identification of species. The following treatment of *Leitneria eocenica*, with its synonyms, will illustrate this and other points.

SYSTEMATIC DESCRIPTION

LEITNERIA EOCENICA (Berry) Brown, n. comb.

Pl. 58, figs. 3–6

Capparis eocenica Berry, 1916, p. 218, pl. 44, figs. 1,2 [not fig. 3]; pl. 52, fig. 5.
Capparis eocenica ampla Berry, 1930, p. 71, pl. 36, figs. 4,5.
Anacardites marshallensis Berry, 1916, p. 261, pl. 58, fig. 6.
Carapa eolignitica Berry, 1916, p. 253, [not pl. 55, fig. 4; pl. 60, fig. 4]; 1930, p. 95, pl. 39, fig. 10.
Diospyros wilcoxiana Berry, 1916, p. 334, pl. 101, fig. 2 [not fig. 1]; 1930, p. 128, pl. 47, fig. 3.
Dodonaea wilcoxiana Berry, 1916, p. 270, pl. 38, fig. 2.

EXPLANATION OF PLATE 58

All figured specimens are in the U. S. National Museum

FIGS. *1,2*—Leaves of the existing corkwood, *Leitneria floridana* Chapman, showing aberrant secondary venation.
3–6—*Leitneria eocenica* (Berry) Brown, n. comb. *3*, U.S.G.S. loc. 6467, Holly Springs, Miss. Reproduction of *Dodonaea wilcoxiana* Berry, 1916, pl. 38, fig. 2. *4*, U.S.G.S. loc. 9077, Viola, Ky. *5*, U.S.G.S. loc. 8619, Grable pit, Henry Co., Tenn. *6*, U.S.G.S. loc. 6456, Puryear, Tenn. Reproduction of *Diospyros wilcoxiana* Berry, 1930, pl. 47, fig. 3.

Myrcia parvifolia Berry, 1916, p. 315, pl. 90, fig. 1.
Schefflera? elliptica Berry, 1930, p. 124, pl. 41, fig. 10.

In the foregoing synonymy of 8 species distributed among 7 genera in 7 different families (*Capparis*, caper family, Capparidaceae; *Carapa*, mahogany family, Meliaceae; *Anacardites*, sumac family, Anacardiaceae; *Diospyros*, ebony family, Ebenaceae; *Dodonaea*, soapberry family, Sapindaceae; *Myrcia*, myrtle family, Myrtaceae; *Schefflera*, ginseng family, Araliaceae), no *Leitneria* is listed. That all, however, as the reader may verify by studying Berry's illustrations of the leaves, belong to one genus and species and that, on both morphologic and ecologic grounds, they are assignable to *Leitneria*, seems clear when they are compared with the existing corkwood, *Leitneria floridana* Chapman (pl. 58, figs. 1,2).

Whether large or small, these leaves have a number of significant features in common. They are elliptic in outline, rounded to blunt-pointed at the apex, cuneate at the base, with thick petioles. The midveins are heavy. From them branch numerous camptodrome secondary veins in fairly regular fashion but strikingly, in most specimens some aberrant ones branch off at notably different angles than the rest. This singularity, in combination with the other characteristics mentioned, makes it relatively easy to spot these leaves.

The living *Leitneria floridana*, a monotypic species, is a shrub or small tree, growing in swamps at isolated localities in the southern States, specifically, according to C. S. Sargent's *Manual of the trees of North America*, 1933, along the lower Altamaha River, Georgia; on the Gulf Coast from the Apalachicola River, Florida, to the Brazos River, Texas; Lincoln and Clay counties, Arkansas; and Butler and Dunklin counties, Missouri. Growing in swampy sites the corkwood is admirably situated for leaving remains in the fossil record. The swamps and sloughs around the Mississippi embayment in Eocene time provided such a habitat and it is not surprising, therefore, that remains of *Leitneria* are widespread in the Wilcox-Claiborne strata. Thus far, however, no authentic seeds of *Leitneria* have been reported from the Eocene of the southern States, but I predict with confidence that they will be found if an intensive search be made at appropriate leaf localities, such as the clay pits near Puryear, Tennessee, and at Viola, Kentucky. I, myself, have not had an opportunity to make this search, for the idea that the leaves in question might be those of *Leitneria* did not occur to me until long after my last visit into the area.

Although Berry (1916) made a lengthy statement about the composition of the Eocene flora, he did not give a concise summary of the species now living in the Gulf Coast region, and especially of those that might be good prospects for preservation as fossils. The fact that he did not identify *Leitneria* in the Eocene flora is perplexing for only a year later he reported probable winter buds of corkwood from Recent deposits near Vero, Florida (1917, p. 23).

Berry's failure to recognize as a single species of *Leitneria* all of the items listed in the synonymy prompts a closer look at some of them for other possible errors. If these leaves are intimately related by having a number of characteristic features in common, how did Berry manage to distinguish 7 different genera among them? Why did he not identify some as *Kalmia* and *Rhododendron?* Or the leaflets of *Psidium?* Homomorphy or convergence of characters in widely separated families is recognized, particularly in those with entire leaves; but, considering all the attendant circumstances, is this tendency common enough to cause multiple misidentifications by a trained morphologist? Let the reader discover for himself the answer to these questions by reading Berry's descriptions and determining whether or not he detected and reported valid differences as a basis for his identifications.

Berry stated (1916, p. 219) rather confidently that the leaves of his *Capparis eocenica* "can scarcely be distinguished from those of *C. domingensis* Sprengel." Actually, the resemblance is only superficial, as close inspection will disclose to the student capable of and seriously interested in making the comparison. His figures 1 and 2, plate 44, are clearly illustrations of leaves of a single species, but his figure 3 is just as clearly of something different. Figures 1 and 2 show the aberrant secondary venation of *Leitneria*, but figure 3 shows no such

venation. On magnification, the petiole is distinctly glandular and cross-wrinkled and thus, with its other features, is highly suggestive of being a leguminous leaflet.

To which of the numerous legumes identified by Berry in the Eocene flora does this leaflet belong? What about the identity of his legumes? Here we run headon into difficulties and confusion. Compare his plate 47, figure 12 (*Sophora wilcoxiana* Berry) with plate 95, figure 5 (*Laguncularia preracemosa* Berry); and his plate 47, figure 13 (*Sophora wilcoxiana* Berry) with plate 95, figure 6 (*Laguncularia preracemosa* Berry). The two specimens compared in each couplet are counterparts! *Sophora* is a genus of legumes but *Laguncularia* is a so-called white mangrove far removed in classification from the legumes. Nevertheless, all these specimens are legumes, with cross-wrinkled, glandular petioles. Further, if these specimens are to be called *Sophora wilcoxiana* the latter will have to include other specimens Berry identified as *Cassia*, *Cedrela*, *Gleditsiophyllum*, *Mimosites*, and *Sapindus*!

In his 1930 revision of the Eocene flora Berry described 2 leaf species of *Menispermites*—*M hardemanensis* Berry (p. 69, pl. 10, fig. 2) and *M. americanus* Berry (p. 69, pl. 11, figs. 1–4); *Zygophyllum? eocenicum* Berry (p. 94, pl. 31, fig. 1); *Leguminosites drepanocarpoides* Berry (p. 86, pl. 12, figs. 11, 12); and 3 species of pods—*Cladrastis eocenica* Berry (p. 84, pl. 41, fig. 12), *Parkinsonia eocenica* Berry (p. 77, pl. 12, fig. 9; pl. 41, fig. 11), and *Leguminosites collinsi* Berry (p. 89, pl. 13, figs. 6, 7; pl. 22, fig. 5; pl. 41, fig. 20). In no instance, however, did he refer to the leguminous genus *Erythrina*. Nevertheless, all of the foregoing items seem clearly referable to this genus. The deltoid to hastate leaflets, with their cross-wrinkled petioles, and the pods, with constrictions between the seeds, can be matched fairly closely against the similar organs of the coral-bean, *E. herbacea* Linnaeus, and its variety, *arborea* Chapman. In 1951 I collected specimens of this native legume on the shores of Tampa Bay, Florida.

Further confusion of legumes and other things is illustrated by the treatment of *Mimusops mississippiensis* Berry (1916, p. 340, pl. 108, fig. 1) and *Metopium wilcoxianum* Berry (1916, p. 260, pl. 57, fig. 3). Both have the cross-wrinkled, glandular petioles and the characteristic venation of legumes, whereas *Mimusops* and *Metopium* are genera in other families. On the other hand, *Metopium wilcoxianum* Berry (1916, p. 260, pl. 101, figs. 1,3) is clearly assignable to *Diospyros wilcoxiana* Berry (1916, p. 334, pl. 101, figs. 1,3), which has the appearance of being a true persimmon.

Berry had considerable artistic skill and liked to publish restorations of fossil plants, as witness the numerous text figures in his 1930 U. S. Geological Survey Prof. Paper 156. One of these, figure 9, a restoration of a palm, *Sabalites grayanus* (Lesquereux) Berry, needs comment for it illustrates further his oversight of significant morphological detail. The drawing was intended to represent both the upper and under sides of the leaves, but the observer will note that all the leaves have long, narrow, wedge-shaped projections (hastulae) of the petioles into the fans. In living species of *Sabal*, however, the long projection is on the under side, whereas that on the upper side is short and blunt. Good counterparts of a fossil *Sabal* leaf also show this feature plainly. When I pointed out to him this discrepancy in his sketch Berry jocosely remarked, "Oh, that was poetic license!"

When it fell to my lot in 1945 to curate all the Berry paleobotanical material not theretofore donated by the Johns Hopkins University to the U. S. National Museum, I found in the Eocene collections from the Gulf States two fragments of leaves, one (U.S.N.M. 36308) identified as *Nectandra lancifolia* (Lesquereux) Berry, and the other (U.S.N.M. 36303) as *Rhamnus coushatta* Berry, species in unrelated families; but these pieces fitted together readily and made a nearly complete leaf!

Aside from the foregoing and many other misidentifications in the Eocene flora, Berry erred seriously on at least two other occasions. In 1924 he described an object from Texas as a fossil gourd, *Calycophysoides balli* Berry. When I discovered that this specimen is an artifact called a Cape Cod firelighter and told him about it he very graciously made the correction (1937). In 1929 (p. 8, pl. 1, figs. 13,14) he described what he supposed was the first fossil choco-

late-bean pod, *Theobroma fossilium* Berry, from Colombia, South America. This I found to be the forepart of a reptilian jaw, the remnants of its teeth having been mistaken for seeds.

In 1940 and 1944 when I started to do something about the confused state of the Eocene flora of the southern States Berry (1945) responded with generalized diversionary objections and the somewhat sarcastic remark that "if science [that is, paleobotany] is not to become a joke its votaries must refrain from making changes in which opinions and not facts are allowed to assume so leading a role." Precisely, but let its votaries also profit from past mistakes and refrain from rushing into print with half-baked observations and identifications that are later excused as inadvertencies and poetic license. Let it be entirely clear that this recitation of errors is not intended to besmirch Berry's great reputation and his character. He was my friend and teacher to whom I owe very much.

Why did I not prepare a complete revision of the Eocene flora when I had all the specimens at my elbow in the U. S. National Museum? I can answer this question, at least to my satisfaction. In 1929 when I became the paleobotanist of the U. S. Geological Survey for Mesozoic and Cenozoic floras I found the collections of those types and supplementary specimens at the U. S. National Museum in such unworkable condition that I had to devote a large part of my time to extensive curating before I deemed that good research could be done with them. This and the need for much field work to collect more material and to establish correct stratigraphic sources for many of the Paleocene collections with which I was more directly concerned, occupied me so steadily that I had no time for the restudy of the Eocene flora. Here, however, is a flora that needs and deserves concentrated attention.

REFERENCES

BALL, OSCAR M., A contribution to the paleobotany of the Eocene of Texas. 1. Agric. and Mech. College of Texas Bull., 4th ser., v. 2, no. 5, p. 1–173 .

——, 1939, 2, *idem*, v. 10, no. 3, p. 1–54.

BERRY, EDWARD W., 1916, The lower Eocene floras of southeastern North America. U. S. Geol. Survey Prof. Paper 91, p. 1–481.

——, 1917, The fossil plants from Vero, Florida. Florida Geol. Survey Ann. Rept., p. 19–33.

——, 1922, Additions to the flora of the Wilcox group. U. S. Geol. Survey Prof. Paper 131, p. 1–21.

——, 1924, A cucurbitaceous fruit from the Tertiary of Texas. Torreya, v. 24, p. 5–7.

——, 1929, Tertiary fossil plants from Colombia, South America. U. S. Nat. Mus. Proc., v. 75, art. 24, p. 1–12.

——, 1930, Revision of the lower Eocene Wilcox flora of the southeastern States. U. S. Geol. Survey Prof. Paper 156, p. 1–196.

——, 1937, A correction. Torreya. vol. 37, p. 108.

——, 1941, Additions to the Wilcox flora from Kentucky and Texas. U. S. Geol. Survey Prof. Paper 193, p. 83–99.

——, 1945, The lower Eocene flora of southeastern North America. Jour. Washington Acad. Sci., v. 35, p. 87–89.

BROWN, ROLAND W., 1940, New species and changes of name in some American fossil floras. Jour. Washington Acad. Sci., v. 30, p. 344–356.

——, 1944, Temperate species in the Eocene flora of the southeastern United States. Jour. Washington Acad. Sci., v. 34, p. 349–351.

SHARP, AARON J., 1951, The relation of the Eocene Wilcox flora to some modern floras. Evolution, v. 5, no. 1, p. 1–5.

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JOURNAL OF PALEONTOLOGY, V. 34, NO. 3, P. 433–439, PLS. 59–60, 2 TEXT-FIGS., MAY, 1960

PELECYPODS OF THE GENUS *PTEROTRIGONIA* FROM THE WEST COAST OF NORTH AMERICA

DAVID L. JONES[1]
U. S. Geological Survey, Menlo Park, California

ABSTRACT—Three species of *Pterotrigonia* from Cretaceous rocks of the west coast of North America, *P. evansana* (Meek), *P. klamathonia* (Anderson), and *P. oregana* (Packard), are redescribed and figured. *Trigonia inezana* Packard and *T. churchi* Anderson are considered to be synonyms of *P. evansana*. *T. deschutesensis* Packard is considered to be a synonym of *P. oregana*.

P. evansana ranges from the Coniacian to the Campanian; *P. klamathonia* ranges throughout the Turonian, and *P. oregana* ranges from lower or middle Albian to about upper Cenomanian.

INTRODUCTION

TRIGONID pelecypods belonging to the genus *Pterotrigonia* van Hoepen are locally abundant in Cretaceous rocks of the west coast of North America, but they have received little detailed study since Packard's (1921) monograph on "The Trigoniae from the Pacific Coast of North America." Some species have never been adequately defined or figured, and confusion exists concerning the proper names to be applied. Also, their geologic ranges previously had not been adequately established and their use as stratigraphic markers consequently was diminished.

Since publication of Packard's monograph, the taxonomy of the trigonids has undergone much revision, due mainly to the work of van Hoepen (1929), Crickmay (1932), Dietrich (1933), Cox (1952), and Kobayashi and co-workers (1954, 1956, 1957). A great proliferation of new generic and subgeneric names resulted from this work, with little agreement among the various workers as to the validity of many of these new names. The species that Packard originally assigned to the Aliformis subgroup of Agassiz's Scabrae group are now placed in the genus *Pterotrigonia* van Hoepen (Kobayashi and Nakano, 1957, p. 225, 226). Of the five species and varieties referred to this subgroup by Packard, four are discussed in this report. No specimens of the fifth species, *Trigonia columbiana* Packard, have been collected by the writer, so nothing new can be added to its original description at this time.

Large numbers of pterotrigonids were collected by the writer while mapping Upper Cretaceous rocks in the Yreka-Hornbrook area, northern California and southern Oregon. Additional collections were obtained in central Oregon and on Vancouver Island; these were supplemented by older collections of the U. S. Geological Survey, particularly those from the Santa Ana Mountains, southern California, and from southern Oregon. Many specimens in all of these collections can be accurately dated by reference to associated ammonites, and their study has resulted in a clearer understanding of the morphology of the different species and a more accurate delimitation of their stratigraphic ranges. The known ranges are shown on text-figure 1.

The localities from which the figured specimens were obtained are described in the following table and shown on the map, text-figure 2.

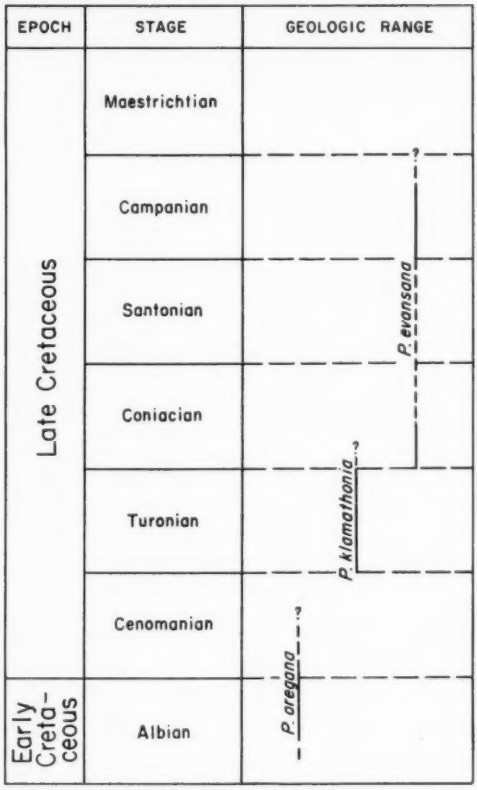
LOCALITIES OF FIGURED SPECIMENS
U. S. GEOLOGICAL SURVEY
MESOZOIC LOCALITIES

No locality number; A on locality map: Vancouver Island, near Nanaimo, exact locality unknown. Coll.: J. S. Newberry, date unknown.

No locality number; B on locality map: Central Oregon, Crooked River, probably South fork of Beaver Creek, exact locality unknown. Coll.: W. P. Blake, date unknown.

2190: Grave Creek, Jackson County, Oregon,

[1] Publication authorized by the Director, U. S. Geological Survey.



TEXT-FIG. *1*—Geologic ranges of pterotrigonias from the west coast of North America.

in sandstone, 50′ to 100′ above base; NE¼SE¼, sec. 6, T. 34 S., R. 5 W. Coll.: T. W. Stanton, 1900.

2212: Jackson County, Oregon, Ashland 15′ quad. ¼ mile north of Siskiyou Station. Coll.: T. W. Stanton, 1900.

17852: Jackson County, Oregon, Ashland 15′ quad., road cut on west side of U. S. Highway 99, NW¼, sec. 24, T. 39 S., R. 1 E. Coll.: F. G. Wells, 1938.

25228: Jackson County, Oregon, Ashland 15′ quad., SE¼, sec. 17, T. 40 S., R. 2 E., on west side of U. S. Highway 99. Coll.: R.W. Imlay, 1954.

26709: Crook County, Oregon, Dayville 30′ quad., NW¼, sec. 12, T. 17 S., R. 25 E., 3,000′ NE of Andrew Bernard ranch house, in first gully entering unnamed creek that flows into S. fork of Beaver Creek. Coll.: R. W. Imlay, 1957.

M-302: Siskiyou County, California, Hornbrook 15′ quad., sec. 7, T. 47 N., R. 6 W., 1,250′ E., 2,650′ N., SW cor.; small hill on east side of Cottonwood Creek, north of bridge, 30′ to 40′ above creek. Coll.: D. L. Jones, 1957.

M-320: Jackson County, Oregon, Ashland 15′ quad., sec. 16, T. 40 S., R. 2 E., 100′ E. 400′ N. SW cor., about 2½ miles north of Siskiyou Summit on west side of U. S. Highway 99. Coll.: D. L. Jones, 1958.

M-321: Crook County, Oregon, Dayville 30′ quad., sec. 11, T. 17 S., R. 25 E., 50′ W., 1,700′ S., NE cor., in small gully entering unnamed tributary of south fork of Beaver Creek. Coll.: D. L. Jones, 1958.

M-322: Crook County, Oregon, Dayville 30′ quad., sec. 11, T. 17 S., R. 25 E., on secondary tributary to south fork of Beaver Creek, 1,100′ upstream (North) from junction with primary tributary, ¼ mile NE of Andrew Bernard ranch house. Coll: Lawrence Vigrass, 1956.

M-323: Vancouver Island, B. C., Nanaimo Lakes 1:50,000 topographic map 92 F/1 East, Mountain District, Flynnfall Creek (Brannen Creek) about 1 mile upstream from junction with Brannen Lake. Coll: D. L. Jones, 1958.

M-324: Vancouver Island, B. C., Nanaimo Lakes 1:50,000 topographic map 92 F/1 East, Mountain District, Flynnfall Creek (Brannan Creek) about 1½ miles upstream from junction with Brannen Lake. Coll: D. L. Jones, 1958.

M-325: Vancouver Island, B. C., Elkhorn Creek, tributary to Nanaimo River, Nanaimo 1:50,000 topographic map 92 G/4 West half, about ¼ mile upstream from junction with Nanaimo River, in float. Coll.: D. L. Jones, 1958.

M-328: Siskiyou County, California; Hornbrook 15′ quad., sec. 7, T. 47 N., R. 6 W., 1,850′ E., 1,050′ N., SW cor., 20′ south of bridge across Cottonwood Creek, in rock blasted out for bridge foundation. Coll.: D. L. Jones, 1958.

No locality number; C on locality map: Santa Ynez Mountains, Santa Barbara County, California. Exact locality unknown. Holotype of *Trigonia inezana* Packard, Univ. California no. 31464. Coll.: E. L. Packard, date unknown.

M-329: Orange County, California, Black Star Canyon 7½′ quad., sec. 31, T. 4 S., R. 7 W. 2,425′ N., 225′ E. af SW cor. Top of Holz shale. Coll.: Jack Vedder, 1950.

N-330: Butte County, California, Paradise 15′ quad., sec. 23, T. 23 N., R. 2 E., on west bank of Big Chico Creek. Coll.: D. L. Jones, 1954.

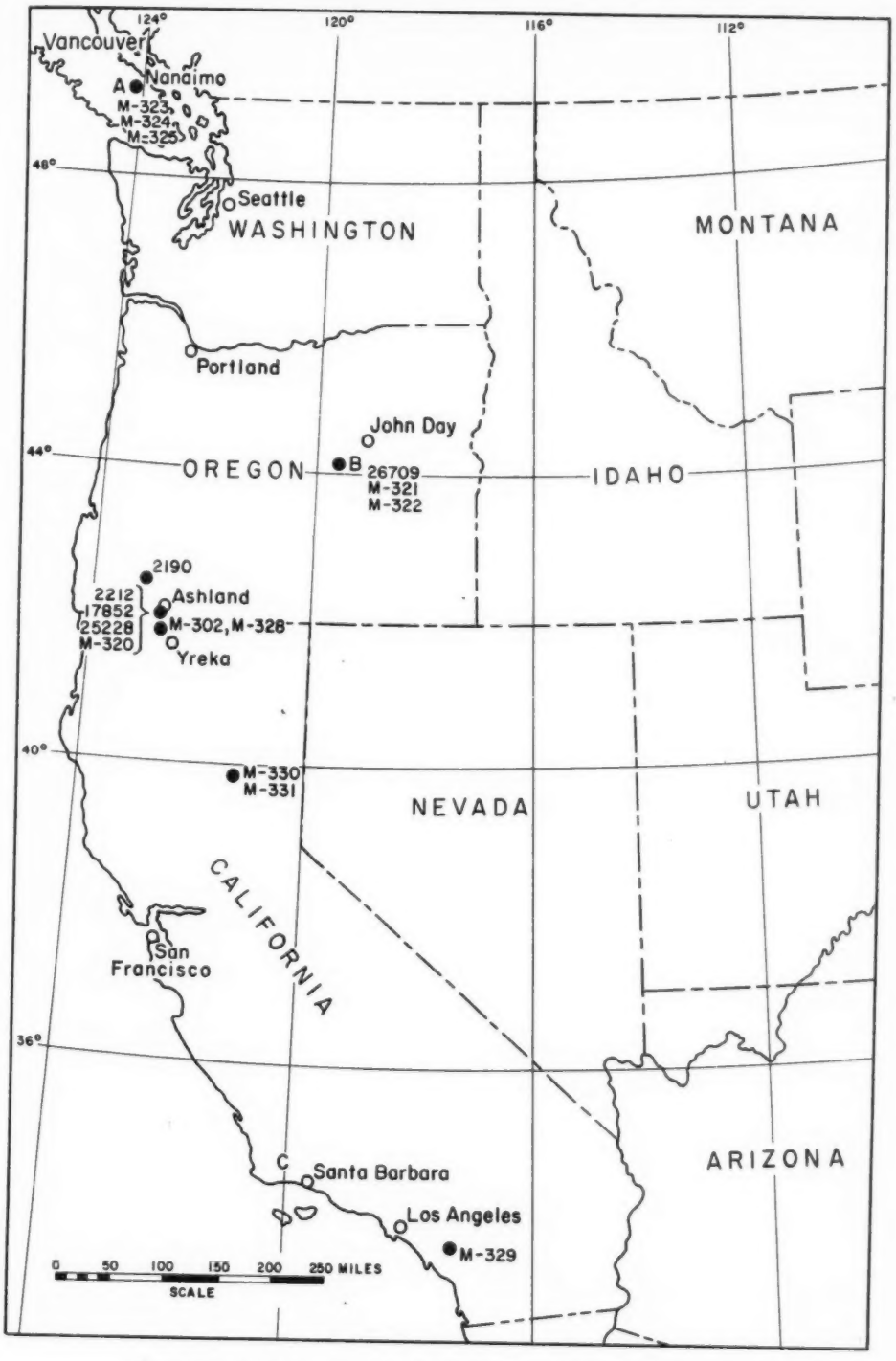
M-331: Butte County, California, Paradise 15′ quad., 3 miles northeast of concrete bridge over Big Butte Creek, on west bank of Butte Creek. Coll.: Rufus E. Cook, 1947.

SYSTEMATIC DESCRIPTIONS

Class PELECYPODA

Genus PTEROTRIGONIA van Hoepen 1929

Type species (original designation): *Pterotrigonia cristata* van Hoepen, 1929.



TEXT-FIG. 2—Index map showing localities of figured specimens.

PTEROTRIGONIA EVANSANA (Meek)
Pl. 59, figs. 6,7,12,15;
pl. 60, figs. 1–11

Trigonia evansana Meek, 1858, p. 42; Gabb, 1869, p. 247; Whiteaves, 1879, p. 161; Branner, Arnold, and Newsom, 1909, pl. 2, fig. 5; Stewart, 1930, p. 93; Anderson, 1958, p. 114 (in part).
Trigonia evansi Meek, Gabb, 1864, p. 189, pl. 25, fig. 177 (as *T. evansii*); Meek, 1876, p. 359, pl. 2, fig. 7 (not 7a, 7b).
Trigonia inezana Packard, 1921, p. 27, pl. 8, figs. 1a, b; pl. 9, fig. 1; pl. 10, fig. 1; Popenoe, 1954, p. 18, fig. 8 (as *T. ynezana*); Anderson, 1958, p. 115.
Trigonia churchi Anderson, 1958, p. 115, pl. 17, figs. 6,7.
non-Trigonia evansi Meek, 1876, pl. 2, figs. 7a, 7b.
non-Trigonia evansana Packard, 1921, pl. 9, figs. 5, 6.

Description.—Shell lunate, inequilateral, equivalve, moderately inflated, having greatest convexity in anterior one-third; posterior elongate, compressed. Umbones anterior, narrowly pointed, prominent, strongly opisthogyrate. Anterior margin gently rounded, tending to be flat; ventral and posteroventral margins broadly rounded; dorsal margin concave. Flanks ornamented with 16 to 20 strong, sharp, straight to slightly flexed radiating costae. Large, blunt, tubercles present on anterior costae. Escutcheon broad, depressed, with 16 to 20 well-defined, transverse to slightly oblique, weakly tuberculate costellae. Median dorsal ridge low. Area narrow, bipartite, unornamented except for distinct transverse growth lines.

Discussion.—Confusion exists concerning the relationship of *Pterotrigonia evansana* and *P. inezana* (Packard), due primarily to the lack of adequate illustrations of *P. evansana*. Meek (1876, pl. 2, figs. 7,7a,7b) illustrated two specimens as *Trigonia evansana*, one well preserved, the other nearly unidentifiable. Although Meek did not describe the localities from which these two specimens were obtained, he did state that the species occurs in the "Cretaceous beds at Nanaimo, Vancouver's Island." Meek (1876, p. 360) further stated that: "Mr. William P. Blake also presented to the Smithsonian Institution some masses of rock from Crooked River, Oregon, containing beautiful, sharply-defined moulds of this species." Meek's well preserved specimen which he illustrated on plate 2, figures 7a and 7b, is a gutta percha cast made from one of Blake's Oregon molds, as was previously pointed out by Stewart (1930, p. 93). It is this Oregon specimen that Packard (1921, pl. 9, figs. 5,6) later refigured and cited as the type of *T. evansana*, although he (1921, p. 25) also stated that the holotype is the U. S. National Museum specimen number 12452. This latter specimen is Meek's original figured example from Vancouver Island.

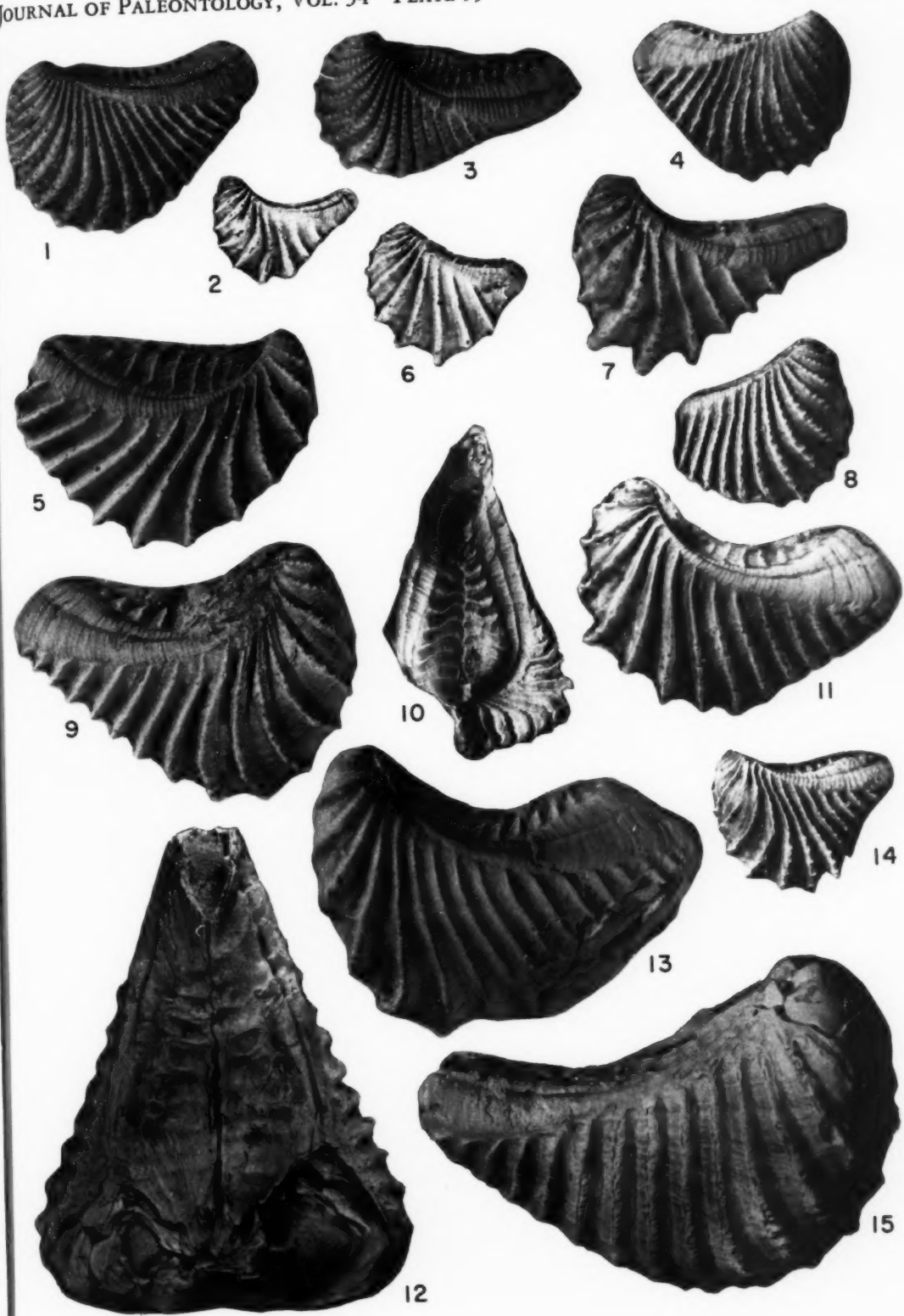
A comparison of Meek's Oregon specimen

EXPLANATION OF PLATE 59
All figures natural size.

FIGS. *1,3,4,8,14*—*Pterotrigonia klamathonia* (Anderson). *1*, left valve, rubber cast of U.S.N.M. No. 130320, from U.S.G.S. Mesozoic Loc. 25228; *3*, left valve, rubber cast of U.S.N.M. No. 130321, from U.S.G.S. Mesozoic Loc. M-320; *4*, right valve, rubber cast of U.S.N.M. No. 130322, from U.S.G.S. Mesozoic Loc. 2212; *8*, right valve, rubber cast of U.S.N.M. No. 130323, from U.S.G.S. Mesozoic Loc. 17852; *14*, left valve, rubber cast of U.S.N.M. No. 130324, from U.S.G.S. Mesozoic Loc. 2212.

2,5,9,10,11,13—*Pterotrigonia oregana* (Packard). *2*, left valve, rubber cast of U.S.N.M. No. 130325, from U.S.G.S. Mesozoic Loc. 2190; *5*, right valve, rubber cast of U.S.N.M. No. 130326, from U.S.G.S. Mesozoic Loc. M-322; *9*, right valve, rubber cast of U.S.N.M. No. 130327, from U.S.G.S. Mesozoic Loc. M-321; *10*, Dorsal view, rubber cast of U.S.N.M. No. 130328, from U.S.G.S. Mesozoic Loc. 28709; *11*, left valve, rubber cast of U.S.N.M. No. 130329, from U.S.G.S. Mesozoic Loc. 26709; *13*, left valve, plaster cast of Meek's (1876) original Oregon specimen illustrated on plate 2, figure 7a, U.S.N.M. No. 7528, index map locality B.

6,7,12,15—*Pterotrigonia evansana* (Meek). *6*, left valve, rubber cast of U.S.N.M. No. 130330, from U.S.G.S. Mesozoic Loc. M-302; *7*, left valve, rubber cast of U.S.N.M. No. 130331, from U.S.G.S. Mesozoic Loc. M-328; *12,15*, Dorsal view and right valve, U.S.N.M. No. 130332, from U.S.G.S. Mesozoic Loc. M-330.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with well preserved specimens of *P. evansana* from Vancouver Island indicates that they are specifically distinct. Thus, the primary distinction made by Packard (1921, p. 27) between *T. evansana* and *T. inezana*, that the former species has a wide bipartite area and the latter species a narrow bipartite area, is not valid because the comparison was made with a much older and morphologically distinct species, not with *T. evansana*.

All of the specimens of *P. evansana* known to the writer from Vancouver Island have a narrow bipartite area, so this feature cannot be used to separate *P. evansana* and *P. inezana*. In other features, such as general outline, size, and in the nature of the ornamentation, the two species appear to be similar. Thus, *P. inezana* is herein regarded as a subjective synonym of *P. evansana*.

P. evansana has a fairly wide range of morphologic variation, particularly in regard to the shape of the costae. These may be nearly straight or slightly sinuous, depending, apparently, on the degree of convexity of the valves. This variation is not thought to be of specific importance.

Age.—On Vancouver Island, Usher (1952, p. 11, 22) records *P. evansana* from the Haslam and Qualicum formations in association with Campanian fossils, including *Canadoceras newberryanum* (Meek) and *Inoceramus schmidti* Michael. According to Popenoe (1954, p. 16, 17, table 1), *P. evansana* (cited as *T. ynesana*) occurs in the Santa Ana Mountains of southern California in the Holz silt and Pleasants sandstone in association with *Metaplacenticeras* sp. and other fossils of Campanian age. In the Yreka-Hornbrook area, northern California, *P. evansana* occurs in rocks of Campanian age, but specimens nearly identical to *P. evansana* also occur with the lower Coniacian ammonite *Prionocycloceras crenulatum* (Anderson) (see pl. 59, figs. 5,6,7). These older specimens appear to have somewhat more widely spaced ribs than do the typical Campanian *P. evansana*, but this variation is not thought to be of specific importance. The known range for *P. evansana* is, thus, from lower Coniacian through the Campanian.

Holotype.—U.S.N.M. no. 12452A.

Type locality.—The exact locality from which Meek's holotype was collected cannot be determined other than probably either from the Haslam or Qualicum formations in the vicinity of Nanaimo, Vancouver Island, British Columbia. The type locality of *T. inezana* Packard is likewise indeterminable, other than from the Santa Inez Mountains, Santa Barbara County, California.

Figured specimens.—U.S.N.M. Nos. 130330–130337, 12452A; U. Cal. 31464, from U.S.G.S. Mesozoic Localities M-302, M-323, M-324, M-325, M-328, M-329, M-330, M-331; index map localities A,C.

PTEROTRIGONIA OREGANA (Packard)
Pl. 59, figs, 2,5,9–11,13

Trigonia evansi Meek, 1876, pl. 2, fig. 7a, 7b.
Trigonia evansana Meek, Packard, 1921, p. 25, pl. 9, fig. 5, 6.
Trigonia evansana var. *oregana* Packard, 1921, p. 26, pl. 9, fig. 7; Stewart, 1930, Phila. Acad. Nat. Sci. Spec. Pub. no. 3, p. 93 (as *T. evansana* var. *oregona*)
Trigonia oregona Packard, Anderson, 1958, p. 116.

EXPLANATION OF PLATE 60
All figures natural size.

FIGS. *1–11*—*Pterotrigonia evansana* (Meek). *1,10*, left valve and dorsal view, U.S.N.M. No. 130333, from U.S.G.S. Mesozoic Loc. M-331; *2,4*, right valve and dorsal view, U.S.N.M. No. 130334, from U.S.G.S. Mesozoic Loc. M-323; *3*, left valve, rubber cast of U.S.N.M. No. 130335, from U.S.G.S. Mesozoic Loc. M-324; *5*, left valve, plastoholotype, U.S.N.M. No. 12452A, index map locality A, Vancouver Island, B. C.; *6,9*, dorsal view and left valve, U.S.N.M. No. 130336, from U.S.G.S. Mesozoic Loc. M-329; *7*, left valve, rubber cast of U.S.N.M. No. 130337, from U.S.G.S. Mesozoic Loc. M-325; *8,11*, dorsal view and right valve, holotype of *Trigonia inezana* Packard, University of California Type Coll. No. 31464, index map locality C.

Trigonia deschutesensis Packard, 1921, p. 24, pl. 10, fig. 3.

Description.—Shell lunate, inequilateral, equivalve, moderately inflated, having greatest convexity in anterior one third. Umbones anterior, prominent, narrowly pointed, strongly opisthogyrate. Anterior margin gently rounded; ventral and posteroventral margins broadly rounded; dorsal margin concave. Flanks ornamented with 15 to 20 strong, sharp, straight to slightly flexed costae separated by concave interspaces. A few small tubercles present on anterior costae. Escutcheon broad, depressed, ornamented with 15 to 20 transverse to oblique costellae. Median dorsal ridge fairly prominent. Area wide, expanding rapidly posteriorly, bipartite, unornamented except for transverse growth lines.

Remarks.—The pterotrigonids found on Beaver Creek (Crooked River), central Oregon have been referred to as *Trigonia evansana*. However, they differ consistently from *P. evansana* in having a much wider area and fewer and finer tubercles on the anterior costae. Because of these differences, the Beaver Creek species deserves a new name. Packard (1921, p. 24, 26) recognized one new species, *T. deschutesensis*, and one new variety, *T. evansana* var. *oregana*, from the Beaver Creek locality. Both of these taxa, together with Meek's original Oregon specimen, appear to constitute one species for which the specific names *oregana* and *deschutesensis* are available. Because the type of *T. evansana* var. *oregana* is better preserved and more typical of the species than is the type of *T. deschutesensis*, the name *oregana* is selected for the Beaver Creek species, despite the fact that *deschutesensis* has page priority.

Stewart's (1930, p. 93) emendation of the specific name *oregana* to *oregona* is not accepted. Although it is probable that Packard meant to name this variety after the state of Oregon, he did not actually state that this was his intention. Thus, no clear evidence exists that the original spelling is in error.

Age.—At its type locality on Beaver Creek in the Suplee area, central Oregon, *P. oregana* is associated with *Desmoceramus* (*Pseudouhligella*) *berryae* (Anderson) of probable lower Cenomanian age. Other Cenomanian fossils, including *Turrilites "oregonensis"* Gabb and *Anthonya* cf. *A. cultriformis* Gabb are abundant 100 to 200 feet below the trigonid locality. On Grave Creek in southwestern Oregon, *P. oregana* occurs with *Megatrigonia* (*Apiotrigonia*) *condoni* (Packard), *Lyelliceras* sp., *Oxytropidoceras* sp., and other fossils of probable middle Albian age. The known range of *P. oregana* is, therefore, from about middle Albian to perhaps middle or upper Cenomanian; the upper limit cannot, as yet, be precisely determined. No evidence is available to indicate that this species occurs in the Senonian as stated by Anderson (1958, p. 109).

Holotype.—Specimen number 4 in the Condon Collection, Department of Geology, University of Oregon, Eugene, Oregon.

Type locality.—University of Oregon Locality 88, Crooked River, Oregon. The exact locality cannot be determined, but as the only place where this species is known to occur on the Crooked River drainage is on the south fork of Beaver Creek, northeast of the Andrew Bernard ranch house (U.S.G.S. Mesozoic Localities 26709, M-321, M-322), it is possible that this is the type locality. The exact locality of Blake's specimen figured by Meek is not known, but possibly it came from this same locality.

Figured specimens.—U.S.N.M. Nos. 130325–130329, 7528, from U.S.G.S. Mesozoic Localities 26709, M-321, M-322, index map Locality C.

PTEROTRIGONIA KLAMATHONIA
(Anderson)
Pl. 59, figs. 1,3–4,8,14

Trigonia cf. *T. evansana* Meek, Popenoe, 1954, p. 18, fig. 6.
Trigonia klamathonia Anderson, 1958, p. 112, pl. 30, fig. 4.

Description.—Shell small to moderate in size, lunate, inequilateral, equivalve; posterior elongate, compressed. Umbones anterior, small, opisthogyrate. Anterior margin gently rounded; ventral and posteroventral margins broadly rounded; dorsal margin concave. Flanks ornamented with 20 to 25 closely spaced, rounded, finely tuberculate costae. Escutcheon slightly depressed, narrow, ornamented with 20 to 25 transverse costellae. Area wide, bipartite,

unornamented except for distinct transverse growth lines.

Remarks.—This species has been commonly mistaken for *P. oregana*. It differs from that species in having more numerous, closely spaced, finely tuberculate ribs. The width of the area of these two species is approximately the same. *P. klamathonia* differs from *P. evansana* (Meek) in having a wider area and more closely spaced, finely tuberculate ribs.

Age.—*P. klamathonia* is abundant in Cretaceous sandstones outcropping south of Ashland, Oregon, where it occurs with the lower Turonian ammonite *Tragodesmoceras ashlandicum* (Anderson). Farther south in the Yreka-Hornbrook area, California, *P. klamathonia* occurs with the upper Turonian ammonite *Subprionocyclus neptuni* (Geinitz). It has not been found by the writer associated with the lower Coniacian "*Prionotropis hiltensis*" (=*Prionocycloceras crenulatum*) as stated by Anderson (1958, p. 112), but at one locality (U.S.G.S. Mesozoic locality M-293) in Rocky Gulch, west of Hornbrook, poorly preserved specimens referable to *P. klamathonia* occur with *P. evansana*. The stratigraphic position of this locality corresponds approximately with that of *Prionocycloceras crenulatum*, so it is possible that *P. klamathonia* occurs occasionally in beds of early Coniacian age.

Holotype.—California Academy of Science Type Coll. no. 10630.

Type locality.—The holotype was found about 4 miles south of Hilt, Siskiyou County, California, on the west side of Cottonwood Creek.

Figured specimens.—U.S.N.M. Nos. 130320–130324, from U.S.G.S. Mesozoic Localities 2212, 17852, 25228, M-320.

LITERATURE CITED

ANDERSON, F. M., 1958, Upper Cretaceous of the Pacific Coast: Geol. Soc. America Mem. 71, 378 p., 78 pls.

BRANNER, J. C., ARNOLD, RALPH, & NEWSOM, J. F., 1909, Description of the Santa Cruz quadrangle [California], U. S. Geol. Survey Atlas, Folio 163.

CRICKMAY, C. H., 1932, Contributions toward a monograph of the Trigoniidae I: Amer. Jour. Sci., 5th ser., v. 24, no. 144, p. 443–464.

DIETRICH, W. O., 1933, Das Muster der Gattung *Trigonia* (Moll. Lam.). Berlin Ges. naturf. Freunde Sitzungsber., no. 4–7, p. 326–332, 1 fig.

GABB, W. M., 1864, Description of the Cretaceous fossils: California Geol. Survey, Paleontology, v. 1, sec. 4, p. 57–217, pls. 9–32.

——, 1869, Description of new, and revision of previously described, Cretaceous fossils: California Geol. Survey, Paleontology, v. 2, sec. 2, pt. 1, p. 127–205.

VAN HOEPEN, E. C. N., 1929, Die Krytfauna van Soeloeland. I. Trigoniidae. Bloemfontein Nas. Mus. Pal. Navorsing, v. 1, pt. 1.

KOBAYASHI, TEIICHI, 1954, Studies on the Jurassic Trigonians in Japan, pt. I, preliminary notes Japanese Jour. Geol. Geography, Trans., v. 25, nos. 1–2, p. 61–80.

——, 1956, Some Jurassic Trigonians from central and west Japan, pt. 5; Japanese Jour. Geol. Geography, Trans., v. 27, no. 1.

——, 1957, A Trigonian faunule from Mindoro in the Philippine Islands: Jour. Fac. Sci. Univ. Tokyo, sec. 2, v. 10, pt. 3.

KOBAYASHI, TEIICHI, & NAKANO, MUTSUO, 1957, On the Pterotrigoniinae. Japanese Jour. Geol. Geography, Trans., v. 28, no. 4, p. 219–238, pls. 16–17.

MEEK, F. B., 1858 [For 1857], Descriptions of new organic remains from the Cretaceous rocks of Vancouver's Island: Albany Inst., Trans., v. 4, p. 37–49.

——, 1876, Descriptions and illustrations of fossils from Vancouver's and Sucia Islands and other northwestern localities: U. S. Geol. Geog. Survey Terr. Bull., v. 2, no. 4, p. 351–374, pls. 1–6.

PACKARD, E. L., 1921, The Trigoniae from the Pacific Coast of North America: Univ. Oregon Pub., v. 1, no. 9, p. 1–58, 11 pls.

POPENOE, W. P., 1954, Mesozoic formations and faunas, southern California and northern Baja California: California Div. Mines Bull. 170, chap. III, p. 15–21, 4 text-figs., 1 table.

STEWART, R. B., 1930, Gabb's California Cretaceous and Tertiary type Lamellibranchs: Philadelphia Acad. Nat. Sci., Special Pub. No. 3, p. 1–314, pls. 1–17.

USHER, J. L., 1952, Ammonite faunas of the Upper Cretaceous rocks of Vancouver Island, British Columbia: Canada Geol. Survey Bull. 21, 182 p., 30 pls.

WHITEAVES, J. E., 1879, Canada Geol. Survey, Mesozoic Fossils: v. 1, p. 2, p. 93–190, pl. 11–20.

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TYPE SPECIES OF *PTILODICTYA*—*PTILODICTYA LANCEOLATA* (GOLDFUSS)

JUNE R. P. PHILLIPS ROSS
Peabody Museum, Yale University, New Haven, Conn.

ABSTRACT—This redescription of the type species of the cryptostome genus *Ptilodictya*, *Ptilodictya lanceolata* (Goldfuss), based on original material and additional specimens discusses zoarial structures and their development.

INTRODUCTION

CERTAIN cryptostome genera at present classified in the families Ptilodictyidae, Stictoporellidae and Rhinidictyidae (Bassler, 1953) have similar structure and development. The phylogenetic relations of these bifoliate genera represented by the type species *Escharopora recta* Hall, *Stictoporella interstincta* Ulrich, *Graptodictya perelegans* (Ulrich) and *G. elegantula* (Hall) are not known but distinctive zooecial wall structure, mode of budding of zooecia, and development of zoaria suggest close relations. This study of *Ptilodictya lanceolata* shows that it has many similarities with this group of genera but the significance of this relation is at present obscure in that our knowledge of their distribution and succession is very incomplete.

Acknowledgments.—I am greatly indebted to Professor Carl O. Dunbar, Peabody Museum, Yale University, for his generous help with this bryozoan study; to Miss Helen Duncan, U. S. Geological Survey, Washington, for her helpful comments; to Dr. R. S. Boardman, U. S. National Museum, Washington, for his kind help, and to Dr. J. Schweitzer, Geologisch-Paläont. Institut, Bonn, Germany, for the loan of material to Peabody Museum. The text-figure is the work of Dr. C. A. Ross, Yale University.

Genus PTILODICTYA Lonsdale 1839

Type species.—*Ptilodictya lanceolata* (Goldfuss) 1826–1833.

PTILODICTYA LANCEOLATA (Goldfuss) 1826–1833

Pl. 61, figs. 1–14; pl. 62, figs. 1–8

Flustra lanceolata GOLDFUSS 1826–1833, Petrefacta Germaniae, v. 1, p. 104, pl. 37, figs. 2a–2d.
Ptilodictya lanceolata (Goldfuss) LONSDALE in Murchison, 1839, Silurian System, p. 676, pl. 15, figs. 11, 11a–11c.

Type material.—Original specimen figured by Goldfuss (1826–33, pl. 37, figs. 2a,2b), no. 283, Geologisch-Paläont. Institut, Bonn, Germany; locality given by Goldfuss "in the region of Groningen, encrinite member of dense grey limestone" (translated from German). Hennig (1905, p. 20) made the note that the original specimens of Goldfuss were found in loose blocks of upper Silurian encrinite limestone at Groningen. Presumably these blocks were found in the glacial drift so that the original locality and precise age of Goldfuss' material cannot be determined, and no topotype material can be collected.

The specimen figured by Goldfuss (1826–1833, pl. 37, figs. 2c,2d) has not been located.

Additional material.—U. S. National Museum nos. 137911A–D, 137912–137914; Silurian, Wenlock, Dudley, England. USNM 137915–137934, Silurian, lower Ludlow, Mulde near Klinteham, Gotland. USNM 137935, Silurian, upper Llandovery Roneham, Gotland.

Description.—Zoarium: This is a flat to subcylindrical slender bifoliate branch without bifurcations. The branch length and branch width vary greatly; young specimens are about 4.5 mm. long and 0.9 mm. wide (USNM 137929) and older, well developed specimens range up to 26 mm. or more in length and are 7.0 mm. wide (USNM 137911).

Zoaria grow from pointed proximal tips and in young specimens the zooecial surfaces consist of a small number of smooth longitudinal ranges (USNM 137929,

137930, 137932). About 1–3 mm. above the proximal tip in older specimens, a sharp annular ridge projects above the zooecial surface (USNM 137911, 137912, 137931, 137933, 137934). This thickened ridge apparently represents the upper part of a joint and the proximal part of the zoarium below apparently articulated in a basal socket. The longitudinal ranges are continuous across the annular ridge.

Zooecia extend the complete width of branches and lateral margins are absent. In some specimens slight elevations develop regularly along the median ranges in the distal part of the zoarium (USNM 137912) but monticules are absent.

The elongate zooecial apertures form well defined ranges which increase in number distally by bilateral subdivision of zooecia in the median ranges (pl. 61, fig. 9). The ranges on a branch may be separated into a distinct median group lying between two lateral groups (pl. 61, fig. 8). Zooecial apertures in the median ranges open directly to the surface and the transverse zooecial walls are at right angles to the lateral zooecial walls. Zooecial apertures in the lateral ranges are oblique to the surface and transverse zooecial walls slope distally outward to the margin of the branch to meet the lateral zooecial walls obliquely.

In the lower proximal part of zoaria, zooecial apertures are smaller and zooecial walls are thicker than in the more distal parts (compare pl. 61, fig. 13, with pl. 61, fig. 9).

Acanthopores and mesopores are absent.

The zooecial microstructures: The zooecium grows from the mesothecal plane as a set of thin walls which are laterally continuous with adjacent zooecial walls. The zooecia bud distally in longitudinal ranges and a small distal pore (0.04 mm. diameter) in the transverse wall connects suprajacent zooecia (pl. 62, fig. 6). Serial sectioning of USNM 137914 provided data on this budding of zooecia in longitudinal ranges. In many zooecia, particularly in the lateral parts of the zoaria, small cysts lie against the mesothecal plane at the base of the zooecial tubes. The lamellate walls of such cysts are continuous into the lamellae of the inner zooecial walls and may represent remnants of a reproductive stage of the zooecia. (pl. 62, figs. 5,6,8).

In their growth outwards and upwards. from the mesothecal plane the zooecial tubes extend for a short distance (about 0.2 mm.) at a low angle of 20° to 25° to the mesothecal plane. They then change direction to make an angle of 55° to 65° with the mesothecal plane. The zooecial walls do not thicken noticeably where the zooecial tubes curve outward and no hemisepta are present. The zooecial wall, uniform in thickness in the mature region, has distally convex lamellae; the lamellae of the inner wall are inclined at a steep angle to the direction of growth of the zooecium and curve gradually outward toward adjacent zooecia to form broad, distally convex lamellae of the outer wall (pl. 61, figs. 11,14; pl. 62, fig. 7). No boundary separates adjacent zooecial walls which are continuous from one zooecium to the next.

The mesothecal plane is a thin bilaminate partition in the central axial part of the zoarium and is present even in the proximal part of the zoarium. However as the mesothecal plane extends laterally toward the edges of the zoarium it loses its bilaminate identity but retains a position in the plane of bilateral symmetry. In these lateral regions the mesothecal plane becomes a band of convex lamellae which are continuous into the lamellate zooecial walls (pl. 62, fig. 4, text-fig. 1). The mesothecal plane where it joins with the early zooecial walls is sometimes pierced by a pore that connects zooecia on opposite sides of the mesothecal plane.

In shallow tangential sections of older, well developed specimens, median ranges, 5–9 in number, lie between lateral ranges, 6–16 in number on each side. In laboratory preparation as the specimens are ground toward the mesothecal plane the number of median ranges diminishes until just above the mesothecal plane only a single median range with direct zooecia remains and all other ranges have distally oblique zooecial outlines. This apparently represents space adjustments of the zooecial tubes during their growth from the mesothecal plane. The median ranges may represent a region of minimal distal growth, the lateral ranges

TABLE 1—TABLE OF MEASUREMENTS

U. S. National Museum Specimens

	137911A 1.5 cm. above proximal tip	137911B 7.5 cm. above proximal tip	137911C 20 cm. above proximal tip	137911D 26 cm. above proximal tip	137912 Sectioned in distal part of well developed specimen	137913 Sectioned in distal part of well developed specimen	137915 Sectioned in proximal part of young specimen	137917 Sectioned in proximal part of well developed specimen	137918 Sectioned in distal part of well developed specimen
Zoarial branch length—mm.	265	265	265	265	75 incomplete	80 incomplete	30 incomplete	9.5 incomplete	26 incomplete
Zoarial branch width—mm.	3	4.5	6.8	7.1	3.5	6.5	2.5–3.8	5.4	5.5
Zoarial branch depth—mm.	1.8	1.8	1.1	1.1	1.4	1.3	1.5	1.6	not det.
Ranges on branch	18	22	33–34	40	20 at least	40–42	about 14–20	about 26	30
No. of median ranges	5	5	5	6	5	8–9	4–5	4–5	4–5
No. of lateral ranges: on ½ zooecial surface	6	9	15	17	not det.	16	5–9	10	12
No. of zooecia/2 mm. Longitudinally: Median	7.3	6.5	7	6.5	5–5.5	7–8	8	6–7	5–5.5
Lateral	6.5	7	6.5	6	not det.	5.5	5	6	5
Laterally: Median	8.5–9	not det.	8–9	8–9	11	13	9	10	11
Lateral	11	9	10.5	10	not det.	9–10	4	10.5–11	10
Transverse zooecial wall—mm. Median region	not det.	.07–.09	.04	.03–.07	.08–0.09	.05–.06	.02–.04	.04	.05–.06
Lateral region	not det.	.03–.07	.03–.04	.03–.07	.08–0.09	.06	.08	.05	.05–.06
Lateral zooecial wall—mm. Median region	not det.	.07–.09	.04–.06	.07–.10	.09–0.10	.06	.05	.05–.06	.04–.05
Lateral region	not det.	not det.	.04–.06	.07	.08–0.09	.05	.04	.04	.02–.04
Zooecial tube diameter—mm. Zooecial aperature—mm.	not det.	not det.			not det.	not det.	0.18	not det.	not det.
Median region	not det.	(.07–0.1) × .23	(.33–.36) × (.13–.16)	(.21–.31) × (.07–.10)	(.22–0.28) × (.10–.12)	(.22–.28) × (.10–.11)	(.22–.24) × .12	(.20–.24) × (.16–.14)	(.26–.32) × (.13–.14)
Lateral region	not det.	.05	(.23–.29) × (.13–.16)	(.31–.36) × (.10–.11)	.24–0.38 × (.09–.11)	(.30–.34) × (.12–.14)	(.30–.34) × (.13–.16)	(.28–.32) × (.14–.16)	(.36–.34) × (.14–.18)
Ratio: Width of mature region of zooecium / Width of zooecium	not det.	.9	.87	.9	.71–0.87	.60–.64	.9	.63	not det.
Angle between zooecial wall and mesothecal plane in immature region	not det.	not det.	not det.	not det.	not det.	not det.	20°	not det.	not det.
Angle between zooecial wall and mesothecal plane in mature region	not det.	not det.	not det.	not det.	not det.	not det.	60°	not det.	not det.

TABLE 1 (*Continued*)

	137919 Sectioned in distal part of young well developed specimen	137920 Sectioned in distal part of young specimen	137921 Sectioned in distal part of well developed specimen	137922 Sectioned in distal part of young well developed specimen	137924 Sectioned in proximal part of well developed specimen	137926 Sectioned in proximal part of well developed specimen	137927 Sectioned in proximal part of well developed specimen	137928 Sectioned in distal part of young specimen	No. 283, Geologisch-Paläont. Institut, Bonn, Germany. Measurements made from external features
Zoarial branch length—mm.	24 incomplete	26 incomplete	12 incomplete	16 incomplete	11–12 incompl.	13 incomplete	12 incomplete	26.5	27 incomplete
Zoarial branch width—mm.	2	1.5–2	3.5	3	3.4	4	3.2	1.7–2.8	3–4
Zoarial branch depth—mm.	.8–1	not det.	.8	.9	.8	.8	.88–.9	.64	.7–1.1
Ranges on branch	18	12	20	17	20	22	20	11–15	25
No. of median ranges	4–5	2–3	5	5	4	7	4	1–4	5
No. of lateral ranges: on ½ zooecial surface	5–6	8	7	6	8	9	7–8	4–6	9–10
No. of zooecia/2 mm. Longitudinally: Median	7	6	6–6.5	7	7	7	7	8	7
Lateral	5.5–7	6	4.5	4.5–5	5.5	5.5–6.5	6–6.5	6	not det.
Laterally: Median region	11	10–11	11	10	12.5	11	10.5	11.5	8–9
Lateral region	13	10–11	11	12	12	10	12	12	not det.
Transverse zooecial wall—mm. Median region	.02	.03–.04	.02–.03	.02	.02–.03	.02	.02	.01–.02	not det.
Lateral region	.03	.03–.04	.02	.02–.03	.02	.02–.03	.02–.03	.02–.03	not det.
Lateral zooecial wall—mm. Median region	.04	.02	.03–.04	.04	.02	.04	.04	.04–.05	not det.
Lateral region	.03	.01–.03	.04	.02–.03	.015	.03–.04	.04–.05	.03	not det.
Zooecial tube diameter—mm.	not det.	not det.	not det.	not det.	not det.	not det.	not det.	not det.	not det.
Zooecial aperture—mm. Median region	(.24–.26) × .14	(.24–.28) × (.14–.15)	(.26–.32) × (.14–.16)	(.26–.28) × (.14–.16)	(.24–.26) × (.12–.14)	(.24–.26) × .14	(.24–.28) × .12	(.24–.26) × (.13–.14)	not det.
Lateral region	(.26–.34) × .14	(.26–.36) × (.16–.17)	(.32–.36) × .14	.34 × .14	(.34–.36) × (.14–.16)	(.22–.34) × (.12–.14)	(.24–.32) × (.10–.16)	(.34–.42) × .14	not det.
Ratio: Width of mature region of zooecium / Width of zooecium	.74	not det.	.79	.78–.82	.83	.75–.085	.80	.75	not det.
Angle between zooecial wall and mesothecal plane in immature region	not det.	not det.	30°	not det.	20°–25°	25°–35°	30°–35°	25°	not det.
Angle between zooecial wall and mesothecal plane in mature region	not det.	not det.	55°	not det.	60°–70°	55°–65°	65°–70°	65°	not det.

representing regions of increasing distal growth with the outermost lateral ranges representing the point of maximal distal growth (see text fig. 1, page 444).

Zooecial apertures are oval and generally when they are large in the median ranges they are small in the lateral ranges and vice versa. The zooecial walls in the median ranges are generally wider than those in lateral ranges and it is interesting to note that the wider zooecial walls occur in the area which may represent minimal distal growth. In tangential sections the zooecial walls are finely laminate (pl. 61, fig. 13). Occasionally in older parts of zoaria, pustules (0.01 mm. diameter) develop on the surface of the zooecial walls; as many as six may be present on one side of a zooecial aperture (pl. 62, fig. 3). However these small deposits are only observed in very shallow tangential sections.

Transverse structures across the zooecial tubes are generally absent. In USNM 137911A about 1.5 cm from the proximal tip, well defined hook-shaped structures project from some of the transverse walls (pl. 61, fig. 10). The lamellae in these structures continue into the lamellae of the inner zooecial walls by making a sharp right angle bend. These structures were not observed in other parts of the zoarium.

Remarks. Lonsdale based his actual description on the genus *Ptilodictya* and type species *P. lanceolata* on material from the Wenlock limestone, western slopes of the Malvern Hills, England, but also referred Goldfuss' material (*Flustra lanceolata*) to this species.

Ptilodictya lanceolata (Goldfuss) is a subjectively defined species which requires more precise definition because of the widespread distribution of the genus in Ordovician, Silurian, and Devonian rocks. The stratigraphic value of the species of this genus cannot be assessed until its zoarial structures and variability of species are fully known. The lectotype of *P. lanceolate* should be chosen from the two syntypes of Goldfuss (1826–1833). This however is not a satisfactory selection as the geological occurrence of Goldfuss' material is in glacial drift and the specimen No. 283, Bonn Museum, Germany, which is split for the most part along the mesothecal plane is poorly preserved. As any other action to define objectively *P. lanceolata* requires application to the International Zoological Commission, this species remains for the present subjectively defined.

The wall structure of *Ptilodictya lanceolata*

EXPLANATION OF PLATE 61

FIGS. *1–14—Ptilodictya lanceolata* (Goldfuss). *1*, external view of Goldfuss' original specimen which is broken across the mesothecal plane. Bonn Museum, no. 283. ×3; *2*, part of the external side view of Goldfuss' original specimen showing the gently curved zooecial tubes which lack transverse structures. Bonn Museum, no. 283. ×20; *3*, smooth proximal tip of a young specimen. USNM 137927. ×10; *4*, proximal tip of specimen with a low annular ridge. USNM 137916. ×10; *5*, proximal tip of a well developed zoarium with annular ridge. USNM 137934. ×10; *6*, proximal tip of zoarium with annular ridge. USNM 137933. ×10; *7*, proximal tip of zoarium with low annular ridge. USNM 137931. ×10; *8*, distal part of a well developed branch with distinctly differentiated median and lateral ranges. USNM 137924. ×6; *9*, deep tangential section showing the increase of ranges by subdivision of a zooecium. USNM 137913. ×50; *10*, part of a longitudinal section through a zooecial tube with a hook-shaped structure projecting from the distal wall. USNM 137911A. ×50; *11*, part of a transverse section showing zooecia leaving the mesothecal plane and continuous lamellate zooecial walls. USNM 137912. ×100; *12*, one half of a longitudinal section showing distinct curvature of the zooecial tubes as they leave the immature region and narrow zooecial walls of the mature region. The mesothecal plane is on the right. USNM 137922. ×50; *13*, shallow tangential section showing two median ranges on the right and four lateral ranges on the left. Section cut in the proximal part of the zoarium. USNM 137911A. ×50; *14*, part of a transverse section showing zooecia leaving the narrow mesothecal plane and zooecial walls with broad distally convex lamellae. USNM 137914. ×100.

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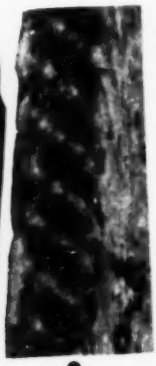
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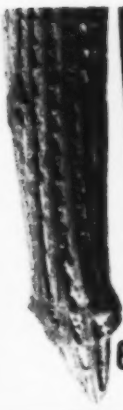
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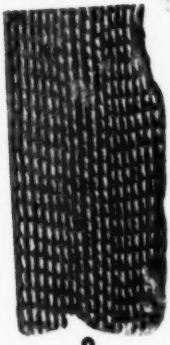
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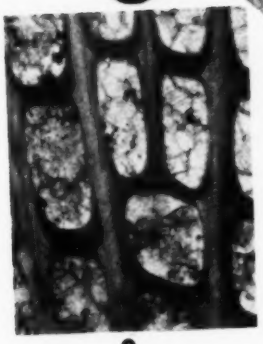
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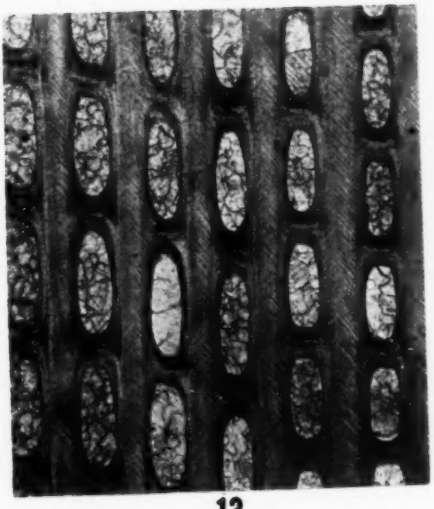
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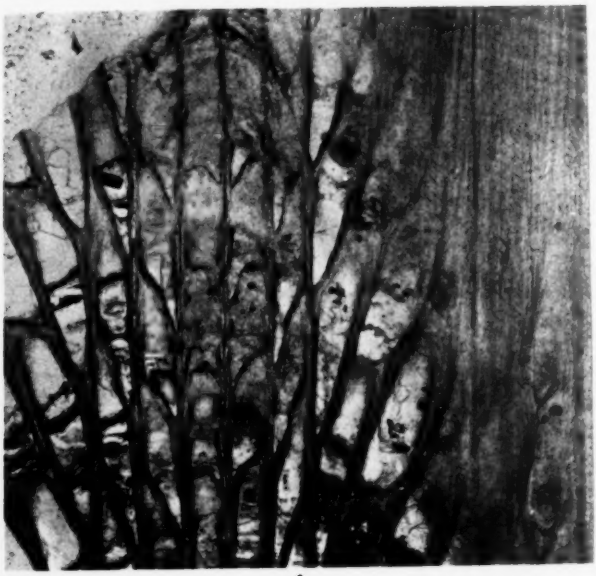

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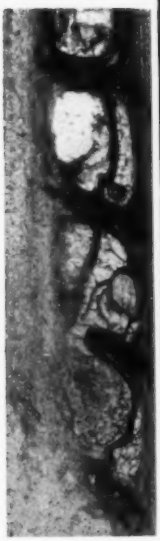

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is similar to that in *Escharopora recta* Hall, *Stictoporella interstincta* Ulrich, *Graptodictya perelegans* (Ulrich) and *G. elegantula* (Hall). The outer zooecial wall of *P. lanceolata* is broader than that in the species mentioned so that the distally convex lamellae of the outer wall have less curvature. *P. lanceolata* is also similar to these species in the development of the mesothecal plane by overlap of the early proximal parts of succeeding zooecial walls.

Both *Ptilodictya lanceolata* and *Escharopora recta* have well developed lamellate lateral extensions of the mesothecal plane but this feature is more strongly developed in *P. lanceolata*. As in *E. recta* and *Stictoporella interstincta* tangential sections of well developed specimens of *P. lanceolata* commonly display pustules on the outer zooecial walls (pl. 62, fig. 3). *P. lanceolata* differs from these species in lacking hemisepta and marked thickening of the zooecial walls in the mature region and having zooecia which are arranged in well defined median and lateral ranges.

Specimens of *P. lanceolata* from the Wenlock limestone of Dudley, England, are more robust, longer, and thicker than specimens from the Ludlovian calcareous clay of Mulde, Gotland. It is not known whether these differences in size are the result of environmental effects or evolutionary changes.

The specimen which Hisinger (1837, p. 104) assigned to *Flustra lanceolata* Goldfuss has generally been placed by later workers in the synonymy of *P. lanceolata*. The external features of this specimen as illustrated by Hisinger (1837) do not appear to compare with Goldfuss' material and it will be necessary to re-examine Hisinger's specimen before a satisfactory identification may be made.

REFERENCES

BASSLER, R. S., 1953, Bryozoa, Pt. G, Treatise on Invertebrate Paleontology: xiii+253 p. The University of Kansas Press, Lawrence, Kansas.

GOLDFUSS, AUGUST, 1826–1833, Petrefacta Germaniae, 128 p. Düsseldorf.

HISINGER, W., 1837, Lethaea Svecica seu Petrificata Sveciae, iconibus et characteribus illustrata, 124 p., 39 pls. Holmia.

HENNIG, ANDERS, 1905, Gotlands Silur-Bryozoer: Arkiv för Zoologi, v. 2, no. 10, p. 1–37, pls. 1, 2.

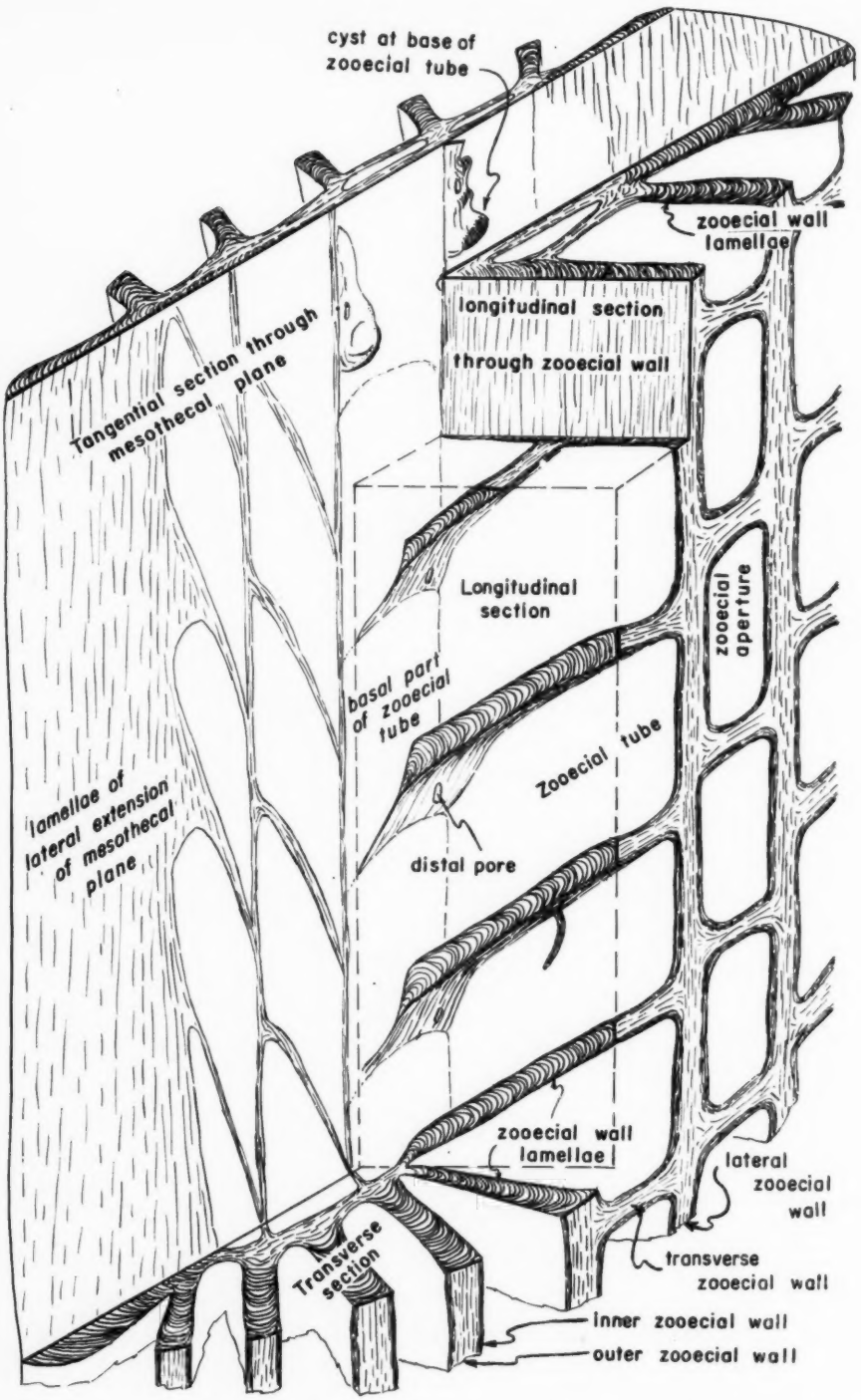
LONSDALE, WILLIAM, 1839, in Murchison, Silurian System, Corals, Pt. 2, p. 275–694.

PHILLIPS, J. R. P., 1960 (in press), Restudy of Types of Seven Ordovician Bifoliate Bryozoa: Palaeontology.

MANUSCRIPT RECEIVED MAY 20, 1959.

EXPLANATION OF PLATE 62

FIGS. *1–8*—*Ptilodictya lanceolata* (Goldfuss). *1*, deep tangential section through the mesothecal plane showing narrow basal zooecial walls in the median ranges and dense lamellae of the outer extension of the mesothecal plane. Lateral zooecial tubes display the typical oblique orientation. USNM 137914. ×50; *2*, transverse section in the proximal part of a zoarium. The narrow part of the mesothecal plane is very short and this quickly gives way to the broad lamellate lateral extensions. USNM 137916. ×50; *3*, shallow tangential section showing lamellate zooecial walls with pustules in the outer walls. USNM 137935. ×50; *4*, transverse section in the lateral part of a zoarium showing lamellate mesothecal plane and zooecial walls. USNM 137911A. ×50; *5*, deep tangential section in the lateral part of a zoarium and approaching the mesothecal plane. The early part of the zooecial tubes are constricted by cysts which develop out of the inner zooecial wall. USNM 137914. ×50; *6*, deep tangential section in the lateral part of a zoarium showing a distal pore connecting adjacent zooecia in the same range. USNM 137914. ×50; *7*, longitudinal section showing a zooecial tube and lamellate zooecial walls which in their basal part leave the mesothecal plane on the right. USNM 137923. ×50; *8*, deep tangential section near the mesothecal plane with the median part of the zoarium near the left. Cysts develop out from the inner zooecial walls and in the lower part of the photograph a pore pierces the zooecial walls. USNM 137914. ×50.



TEXT-FIG. *1*—Diagrammatic sketch of a well developed zoarium of *Ptilodictya lanceolata* (Goldfuss) showing structures in longitudinal, tangential, and transverse sections. ×50 approx.

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MIOCENE COPEPODS FROM THE MOJAVE DESERT, CALIFORNIA

ALLISON R. PALMER[1]
U. S. Geological Survey, Washington, D. C.

ABSTRACT—Fossil copepods are described for the first time. An undetermined cyclopoid species and a harpacticoid assignable to the recent genus *Cletocamptus* are evidence that copepods of modern aspect existed by Miocene time.

INTRODUCTION

COPEPODS are abundant in marine and terrestrial waters throughout the world. Despite their nearly universal present-day distribution in these environments, fossil copepods of modern aspect have never been reported.

A fossil arthropod 145 mm. long from Triassic deposits of the Vosges Mountains was described by Handlirsch (1914) and assigned to a suborder Archeocopepoda of the Order Copepoda. Since no modern copepod exceeds 17 mm. in length (Johnson, 1958) the Triassic fossil on size alone, is atypical of the group. Its close morphologic affinities to the Copepoda have been questioned by Gurney (1931, p. 36).

A subfossil estuarine copepod that retains its original unaltered carapace was recently described from a clay bed six inches beneath a neolithic floor in Kent, England (Harding 1956, p. 1127).

The purpose of this paper is to describe and illustrate for the first time undoubted fossil copepods representing two of the three free-living suborders of this subclass of Crustacea.

The copepods described here are undistorted, silicified specimens with some parts preserved in almost unbelievable detail.

The specimens were obtained from insoluble residues of small calcareous nodules less than 1 inch in diameter (pl. 63, fig. 2) that weather out of the middle part of a 15 foot thick unit of laminated shale in the Barstow formation of middle and late Miocene age in the center NW¼ sec. 26, T. 11 N., R. 1 W., Lane Mountain quadrangle, Mojave Desert, California (USGS Cenozoic locality 21416). The shale, an underlying unit of thin-bedded brown-weathering sandstone, and an overlying unit of thin-bedded gray-weathering sandstone dip steeply to the south and crop out in a series of low knobs that extend for nearly one half mile in an east-west direction a few hundred feet south of the base of a prominent isolated andesite hill that rises about 500 feet above the surrounding desert (pl. 63, fig. 8).

The writer first visited the locality of copepod-bearing nodules in the summer of 1954 at the suggestion of T. W. Dibblee, Jr. and obtained a small collection of nodules. At the time they were not known to be fossiliferous. Poorly preserved but recognizable copepods were discovered in formic acid residues of these nodules in the winter of 1955. The following summer all the nodules weathering from the entire length of the outcrop, amounting to several hundred specimens, were collected. A. M. Bassett, J. A. Patten and R. E. Burkholder, all of the U. S. Geological Survey, assisted in collecting the nodules.

Preliminary information on the fossil copepods was provided by T. E. Bowman of the Division of Marine Invertebrates, U. S. National Museum, Washington, D. C. The writer is particularly indebted to Mildred S. Wilson, Arctic Health Research Center, Anchorage, Alaska, who examined the photographs, critically reviewed the drawings and the manuscript, and provided all information regarding taxonomic affinities of the fossils.

Four male and three female harpacticoid copepods, and three cyclopoid copepods of undetermined sex were recovered from the insoluble residues. In addition, silicified specimens of moderately well preserved fairy shrimp and poorly preserved larvae and pupae of one or two species of Diptera were obtained, similar to those already described in beds of the Barstow formation 10 miles to the southeast (Palmer, 1957).

[1] Publication authorized by The Director, U. S. Geological Survey.

The best preserved specimens are two female harpacticoids that appear to be conspecific. A cluster of eggs beneath the urosome of one of these (pl. 63, figs. 3,6) indicates that the specimen was mature. The second specimen, approximately the same size as the first (pl. 63, fig. 1), has the exopods of all of the legs on the left side, the first and second antennae and the caudal rami preserved.

The male harpacticoids are slightly smaller than the females. On one specimen (pl. 63, fig. 5), the antennules, rostrum and first and second legs on the left side can be resolved. The third leg on the right side of a second male specimen was observed. The males and females each have structures characteristic of *Cletocamptus*, and identical caudal rami. They are considered here to be most likely conspecific.

The cyclopoid copepods are not well enough preserved for comparison in detail with other copepods. Their presence does establish however, that harpacticoid and cyclopoid copepods were already differentiated by Miocene time.

Study of the fossil copepods is particularly difficult because of their small size (largest specimen 0.7 mm. long) and because they cannot be completely cleaned of fine-grained debris or dissected without danger of destroying the entire specimen. For critical examination, the extremely minute structures on the appendages were most clearly shown when a specimen was placed in a dished glass slide and submerged in alcohol or acetone. These liquids, however, have the disadvantage of rapid evaporation causing convection currents within the liquid that often move the specimen. This movement is particularly distracting at the high magnification (about 600 ×)required for study.

The specimens were illuminated from below for study and photography by raising the glass slide about one inch above the microscope base and reflecting a bright spotlight on a sheet of white paper placed below the slide. This method provides much more satisfactory illumination than using a standard arrangement with direct transmitted light from below. Because of the movement of the specimens when submerged in alcohol and acetone, they were submerged in water for photography. Detail drawings of those parts that could be resolved at 600× with a binocular biological microscope were prepared by transferring the image of each part from an ocular grid to graph paper.

SYSTEMATIC DESCRIPTIONS

Class CRUSTACEA
Subclass COPEPODA
Order PODOPLEA
Suborder CYCLOPOIDA
Genus and species undetermined
Pl. 63, figs. 4,7

Material studied.—3 specimens, sex unknown, average length 0.6 mm.

Description.—Prosome (Gooding, 1957, p. 196) broad, subovate in outline, width about 0.25 mm.; length about 0.4 mm.; greatest width at posterior margin of the cephalothorax. Urosome slender, subcylindrical, width about 0.06 mm., length about 0.2 mm. Caudal rami stout, length greater than that of last abdominal segment. Right antenna present on one specimen. Preserved part (which may not be all of antenna) shorter than prosome, without discernible segmentation. No other features of the fossils are resolvable.

Discussion.—These small crustaceans can be definitely placed in the suborder Cyclopoida because of their distinctive body shape, with a broad prosome and a narrow urosome. Absence of knowledge of the appendages prevents any closer identification. The body shape of this species distinguishes it from the associated harpacticoid copepods which have little differentiation in breadth between the prosome and urosome.

Figured specimen.—Incomplete silicified specimen, USNM 563437, from USGS Cenozoic locality 21416.

Suborder HARPACTICOIDA
Family CLETODIDAE
CLETOCAMPTUS sp.
Pl. 63, figs. 1,3,5,6; text-fig. 1

Material studied.—4 ♂, average length between 0.55 and 0.60 mm.; 3 ♀, one with eggs, average length, 0.75 mm.

Description.—Female: Length between

0.7 and 0.8 mm. Body slender, greatest width about one-fourth length. Urosome about three-fifths length of prosome. Genital segment distinctly separated dorsally and at least in part ventrally (pl. 63, figs. 1,3). Surface of cuticle on all body segments smooth. Posterior dorsal margin on each ursomal segment with apparently continuous row of fine, short spinules or hairs. Operculum not apparent, certainly without conspicuous spiny margin. Caudal rami (Text fig. 1d,h) long, slender; width at base slightly less than two-thirds length. Two short outer lateral setae have common base located near proximal part of ramus. Caudal setae consisting of incomplete stout middle seta a little longer than ramus, and part of slender outer seta fused with base of middle seta; usual inner seta not observed. Rostrum well developed, with bluntly rounded apex.

Antennule (text-fig. 1i) composed of at least seven segments; aesthete of segment 4 broken, length not known. Ratio of length of first four segments to length of three terminal segments about 2:1. Antennae composed of at least two segments subequal in length. Four or five setae present on blunt tip of terminal segment.

Mandible, maxilliped and endopods of all legs not resolvable on specimens studied.

Legs 1–3, details not resolvable.

Leg 4 (text-fig. 1a), exopod 3-segmented, outer setae present on distal parts of segments 1 and 2 and medial part of segment 3. At least two long slender apical setae. Comb of short spinules present on outer margin of segment 1.

Leg 5 (text-fig. 1b) outer part of basal expansion with single seta; inner part of basal expansion not completely resolved, but with at least two long slender setae. Exopod not distinctly separated from basal expansion, bearing four terminal setae; outermost and innermost setae broken, the remaining two distinctly unequal in length.

Egg sac with seven large eggs.

Male: Length between 0.55 and 0.60 mm. Body slender, shape similar to that of female. Rostrum well developed (pl. 1, fig. 5); apex bluntly rounded, with hairy margin. Caudal rami as in female.

Antennule (pl. 63, fig. 5) modified and apparently geniculate, segmentation obscured, the part beyond the middle enlarged, the apex narrowed but of indeterminate structure. Antenna (text-fig. 1g) 3-segmented, with at least two long slender terminal setae on segment 3. Two terminal segments subequal in length; longer than basal segment.

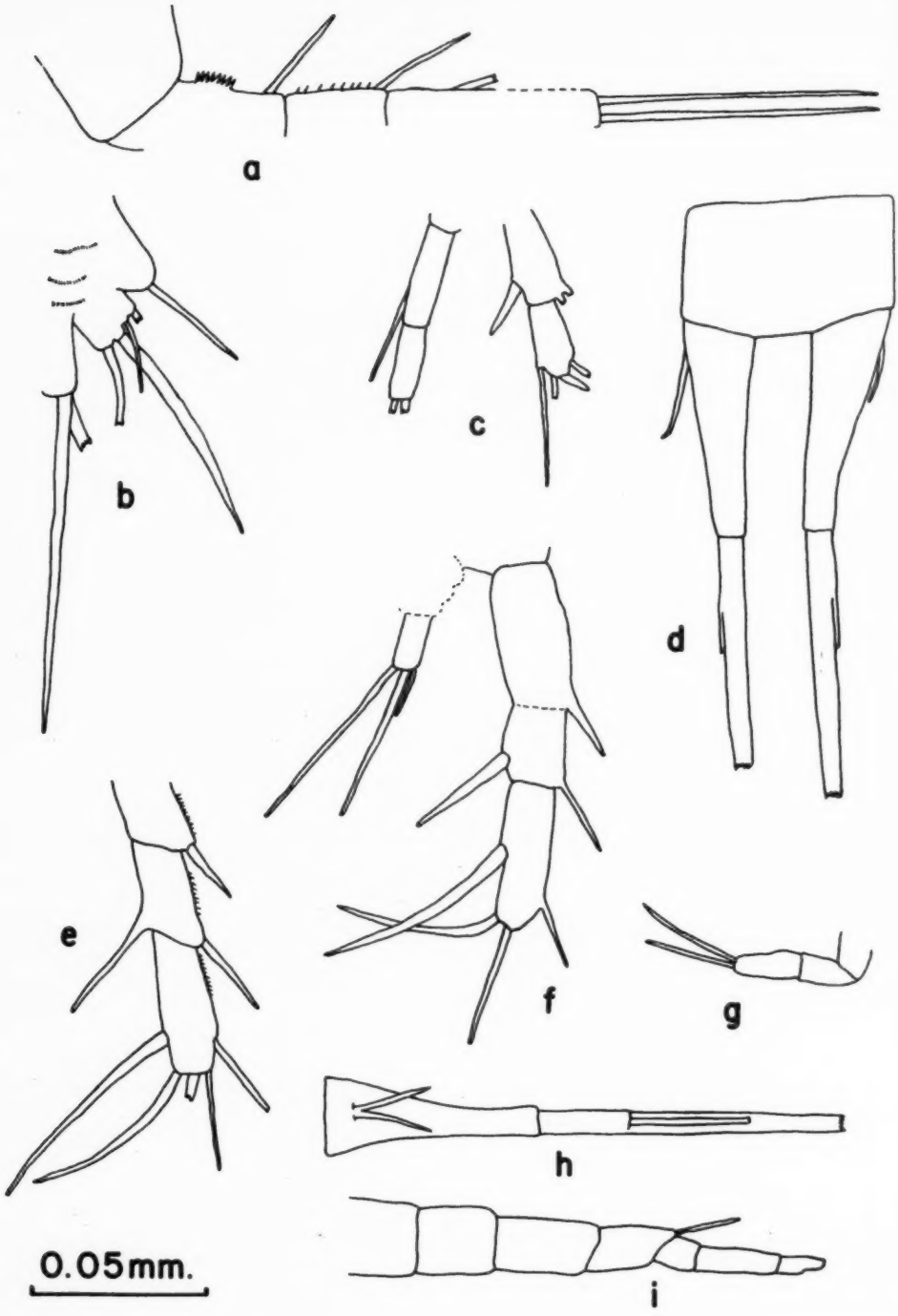
Leg 1 (text-fig. 1c) with exopod presumably 3-segmented (first segment obscured on specimen studied), and endopod 2-segmented. Exopod segment 2 with prominent inner seta; the outer spine not preserved, but two distal prominences present (these represent marginal spinules or segmental processes usually found at the point of insertion of the spine). Segment 3 with four terminal spines or setae. Endopod reaching to near end of exopod; sement 1 with prominent inner seta; segment 2 with at least two terminal setae of indeterminate length.

Leg 2 (text-fig. 1f) with 3-segmented exopod having a prominent spiniform inner seta on the distal parts of segments 2 and 3 and a row of hairs on the inner margin of segment 1. Single stout outer spines present on distal parts of segments 1 and 2. Details of segment 3 not clearly resolved, but appear to be as shown with single outer spine and 2 apical setae. Presence or absence of second outer subapical spine present in known species of *Cletocamptus* could not be determined. Endopod short, about equal in length to segment 1 of exopod; number of segments not certain. Terminal part of last segment with three apical setae, outer one short, spiniform; inner two long, slender, apparently unbroken; innermost seems to be longest.

Leg 3 (text-fig. 1e) with 3-segmented exopod. Single, spiniform inner setae on distal parts of segments 2 and 3; single stout outer spines on segments 1 and 2. Segment 3 with two apparently slender outer spines and two apical setae, inner one curved, outer one broken. Endopod not certainly determined.

Legs 4 and 5 not resolvable on specimens examined.

Discussion.—Most of the characters cited in the description were derived from study of the female and male shown on plate 63, figs. 1 and 5. The specimens are placed with reasonable confidence in *Cletocamptus* on the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following combination of characters: antennule of female 7-segmented, with aesthete on segment 4; female genital segment distinctly separated dorsally; exopod of leg 5 of female not clearly differentiated from the basal expansion; well developed rostrum and the outer and middle caudal setae fused at bases in both sexes; and 2-segmented endopod and 3-segmented exopod of leg 1 of male.

Although a remarkable number of structures are preserved on the fossils, incomplete or lacking information about the following prohibit specific identification: number and lengths of setae and spines on the legs; structure and armature of the endopods of legs 2 to 4 of both sexes, legs 4 and 5 of the male, leg 5 of the female. The fossil species is similar to *Cletocamptus albuquerquensis* (Herrick) in having the outer and middle caudal setae fused at the base. This character distinguishes it from all other western hemisphere species assigned to *Cletocamptus* except *C. dominicanus* Kiefer which has been considered a synonym of *C. albuquerquensis* by Lang (1948, p. 1277). *Cletocamptus retrogressus* Schwankenwitsch, and *C. confluens* (Schmeil), recorded from many parts of Eurasia and North Africa by Lang (1947, p. 1276, 1280), also have this character but differ from the fossil species in having a 6-segmented antennule and much shorter distance of fusion of the caudal setae respectively.

The fossil species differs from *C. albuquerquensis* in having a 7-segmented rather than a 6-segmented antennule, and in having the second endopod segment of leg 1 equal in length only to segment 3 of the exopod rather than to the combined lengths of segments 2 and 3 of the exopod. It is probable that the fossils represent a species related to *C. albuquerquensis*.

In North America, *C. albuquerquensis* is known mostly from inland brackish and saline lakes and ponds in New Mexico, Colorado, Nevada, Utah, Texas, Oklahoma, North Dakota and Saskatchewan; however, some of the reported bodies of water may be fresh and some are recorded as alkaline (M. S. Wilson, written communications Aug. 1958, Jan. 1959). An alkaline environment has been postulated for the aquatic arthropod fauna from the Miocene Barstow formation a few miles south of the copepod locality in the southern Calico Mountains (Palmer, 1957). Fairy shrimp and midges typical of this fauna have been found associated with the fossil copepods.

Figured specimens: Female with eggs, USNM 563435; female with legs of left side preserved, USNM 563434; male, USNM 563436, all from USGS Cenozoic locality 21416.

REFERENCES CITED

GOODING, R. V., 1957, On some Copepoda from Plymouth, mainly associated with invertebrates, including 3 new species: Jour. Marine Biol. Assoc., v. 36, p. 195–221.

GURNEY, ROBERT, 1931, British fresh water Copepoda, Volume 1: 238 p., Ray Society, London.

HANDLIRSCH, ANTON, 1914, Eine interessante Crustaceenform aus der Trias der Vogesen: Wien Verh. zool. bot. Ges., v. 64, p. 1–8, 2 pls.

HARDING, J. P., 1956, A rare estuarine copepod Crustacean, *Enhydrosoma gariensis*, found in

TEXT-FIG. *1*—*Cletocamptus* sp.: a, female, leg 4, exopod; b, female, leg 5; c, male, leg 1, endopod and segments 2 and 3 of exopod; d, female, last body segment, caudal rami and basal parts of fused caudal setae, ventral view; e, male, leg 3, exopod; f, male, leg 2, apex of endopod segment 2 and exopod; g, male, 2nd antenna; h, female, left caudal ramus and fused caudal setae, outer side view; i, female, outline of antennule. Figures a,b,d,h,i from female, USNM 563434, pl. 63, fig. 1; figures c,f from male, USNM 563436, pl. 63, fig. 5; figures e,g from male, USNM 563435, not photographed.

the Holocene of Kent: Nature, v. 178, p. 1127–1128.

HERRICK, C. L., 1895, Copepoda of Minnesota: Geol. and Nat. Hist. Survey of Minnesota, Zool. Ser. 2, p. 41–138, pls. 1–34.

JOHNSON, M. W., 1958, *Bathycalanus sverdrupi* n. sp., a copepod crustacean from the great depths in the Pacific Ocean: Calif. Acad. Sci. Proc., 4th ser., vol. 29, no. 6, p. 257–265.

LANG, KARL, 1948, Monographie der Harpacticiden: v. 2, p. 899–1693,

PALMER, A. R., 1957, Miocene arthropods from the Mojave Desert, California: U. S. Geological Survey Prof. Paper 294-G, p. 237–280, 5 pls., 19 text-figs.

MANUSCRIPT RECEIVED APRIL 22, 1959

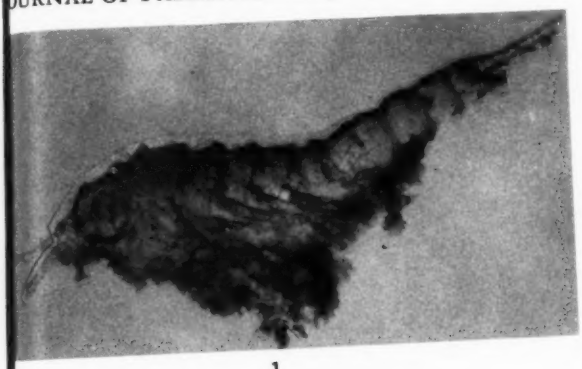
EXPLANATION OF PLATE 63

FIGS. *1,3,5,6*—*Cletocamptus* sp., ×90. *1*, female, left side view, USNM 563434; *3,6*, female, right and left side views showing eggs, USNM 563435; *5*, male, dorsal view showing characteristic antennules and rostrum, USNM 563436.

2—Characteristic nodule from which copepods were obtained, ×2.

4,7—Cyclopoid, genus and species undetermined, ×90. Top and right side views of single specimen, sex undetermined, USNM 563437.

8—Stereophoto of locality of copepod bearing nodules (between arrows) southwestern part of Lane Mountain quadrangle, Mojave Desert, California. Prominent hill is hill 3370.



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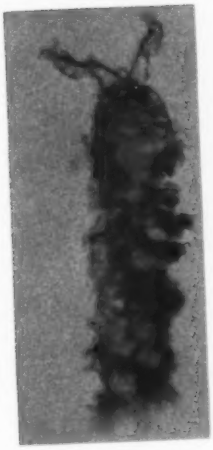

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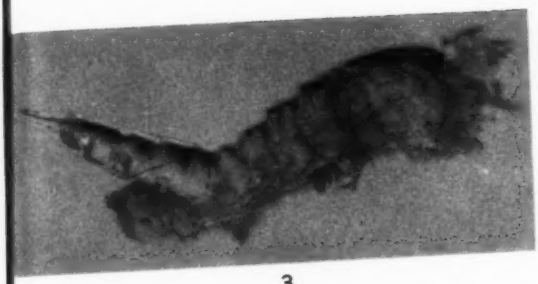

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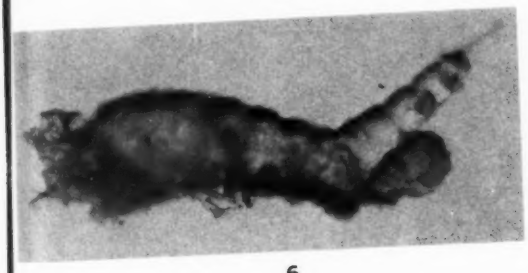

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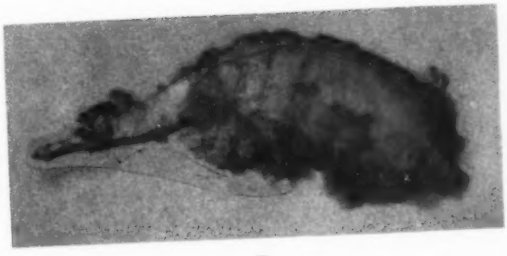

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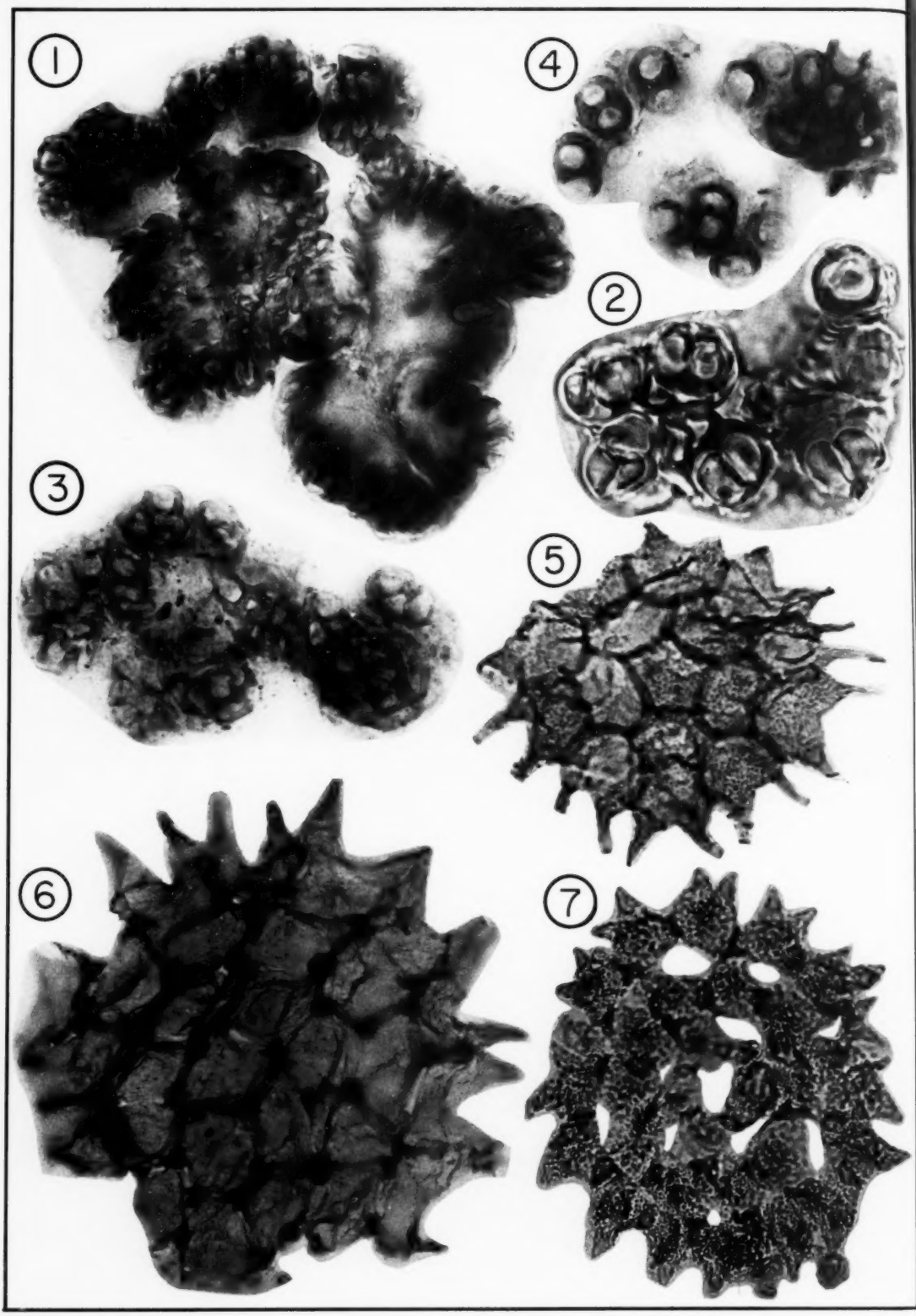
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JOURNAL OF PALEONTOLOGY, V. 34, NO. 3, P. 453–463, PL. 64, 2 TEXT-FIGS, MAY, 1960

FOSSIL CHLOROPHYCEAN ALGAE FROM THE MIOCENE OF OREGON

JANE GRAY
Geochronology Laboratories, University of Arizona, Tucson

ABSTRACT—Two genera of fossil fresh-water algae, *Pediastrum* and *Botryococcus*, and several specimens tentatively referred to *Tetraedron*, are recorded from lacustrine-fluviatile sediments of the late Middle Miocene Mascall formation from the John Day Basin, Oregon, and from strata equivalent in age or somewhat younger from the Blue Mountains to the northeast, and the Stinking Water Basin to the south. The fossil *Pediastrum* and *Botryococcus* are compared with the living species, *P. boryanum*, *P. duplex* and *B. braunii* on the basis of gross morphology. Specimens referred to *Pediastrum* are the first record of this genus in North American Tertiary sediments.

INTRODUCTION

SEVERAL recent papers have focused attention on the geologic longevity of certain microscopic fresh-water members of the Chlorophyta or green algae (Cookson, 1953; Wilson & Hoffmeister, 1953; Traverse, 1955a, 1955b). Lime-secreting members of this division are common fossils in marine sediments and among the important rock makers. Many are well preserved back to the Paleozoic. The fossil record of microscopic fresh-water green algae is only now being documented, however, because of extensive palynological work with all types of sediments. These microscopic forms have firm cell walls composed of extremely resistant cellulose and pectic substances. Essentially the entire organism is thus preserved through millions of years without alteration.

The fossil *Pediastrum*, *Botryococcus*, and *Tetraedron?*, together with specimens resembling *Scenedesmus*, and unicellular chlorococcoid forms similar to *Protococcus*, *Chlorococcus*, *Chlorella*, and others, were discovered while examining for pollen, Miocene diatomaceous ash sediments resting on and interbedded with the Columbia River basalt in east-central Oregon. The lakes and marshes in which these sediments were deposited were formed in irregularities of the basalt surface as the drainage systems were impaired by lava flows and ash falls, and volcanic activity and deformation were increasing the height of the Cascades to the point where they formed a barrier to westward-flowing streams. Plant and animal remains have been collected from these fresh-water sediments for nearly a hundred years, but, other than diatoms, no microorganisms

EXPLANATION OF PLATE 64

Photomicrographs of fossil algae from the Mascall, Blue Mountains and Stinking Water microfloras.

FIGS. *1–2*—*Botryococcus* cf. *B. braunii* Kützing. *1*, Blue Mountains, Oregon (Austin locality), ×750. *2*, Stinking Water, Oregon (loc. P4121), ×970.
3–4—*Botryococcus braunii* Kützing. Specimens from Pleistocene sediments from the Channing Basin, Channing, West Texas. *3*, ×1000; *4*, ×750.
5–6—*Pediastrum* cf. *P. boryanum* (Turpin) Meneghini. Stinking Water, Oregon (loc. P4121). *5*, ×600; *6*, ×750.
7—*Pediastrum* cf. *P. duplex*? Meyen. Stinking Water, Oregon (loc. P4121), ×750.

have been previously noted. Abundant fossil pollen and spores attest to prolific "pollen-rains" from the surrounding vegetation, and the diatoms and other algae suggest that autothonous forms of plant life may have been abundant in these lakes and marshes.

The microfossils have been liberated and concentrated from the ash by means of hydrofluoric acid, Schultz solution (nitric acid and potassium chlorate), and potassium hydroxide. The residue of organic material following this treatment was thoroughly rinsed with water, dehydrated with absolute alcohol, stained with basic fuchsin, and mounted for study in glycerine. Specimens of algae have been isolated in single mount glycerine jelly preparations which will be on permanent file at the Museum of Paleontology, University of California, Berkeley.

Acknowledgements.—I would like to extend special thanks to Drs. G. W. Prescott and G. M. Smith for information about the alga *Pediastrum*, and to Dr. Prescott for critical reading of the manuscript. I would also like to thank Howard Hamman, Jr., and Donald Elkin for assistance in preparing the text-figures and Mrs. Helen Griffin for typing the manuscript.

LOCATION AND AGE OF SEDIMENTS

Microscopic fossil algae are known from the John Day Basin (1); the Blue Mountains (2); the Stinking Water Basin (3) (text-fig. 1). Similarity in the composition of the mega- and microfloras at these localities, as well as in the stratigraphic relations of the basalt and plant-bearing sediments, indicate that the floras from these three areas of the Columbia Plateau are essentially contemporaneous (Chaney, 1959; Gray, 1958).

John Day Basin.—The Mascall formation is a series of predominantly lacustrine-deposited, light-colored ash and tuff beds presently confined in distribution to the valley of the East Fork of the John Day River. The sediments appear to be conformable with the underlying lava, and may be, in part, interbedded with it, although structural conditions have obscured the exact nature of the contact (Merriam, 1901; Thayer & Hay, 1950; Chaney, 1959). The Pliocene Rattlesnake formation unconformably overlies the Mascall.

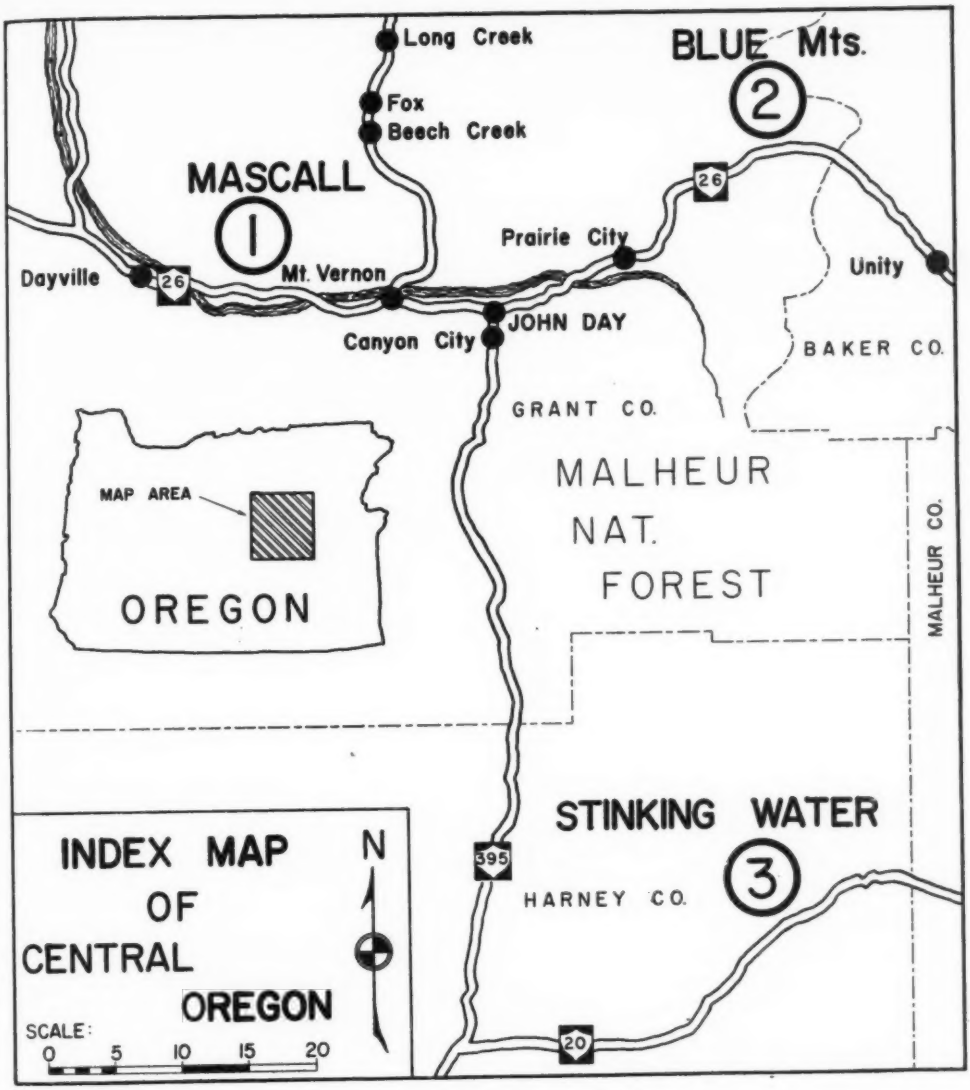
The stratigraphic relations and the relative age of the Mascall formation were first perceived by Merriam (1901), although he did not specify an age, other than Miocene, for the formation. Merriam & Sinclair (1907, p. 197) referred the Mascall "to the middle or later portion of the Miocene," on the basis of faunal and stratigraphic evidence, and Downs (1956, p. 321) has concluded from recent study of the Mascall fauna that it "existed within Hemingfordian (middle Miocene) and Barstovian (late Miocene) time." The plant horizons occur stratigraphically several hundred feet below the mammalian levels, usually within two or three hundred feet of the basal contact of the ash with the Columbia River basalt, or immediately overlying it (Downs, 1956; Chaney, 1959). A late Middle Miocene age appears probable for the Mascall flora.

The two Mascall localities, Meadow and Riverbank, from which algae have been recovered, lie about 900 feet apart, on the north bank of the East fork of the John Day River about 13 miles east of Dayville (U. S. 26), U.S.G.S. Aldrich Mountains Quadrangle, 1943 ed., Grant Co., Oregon.

Blue Mountains.—The Blue Mountains fossil plant localities are within the drainage basin of the Middle Fork of the John Day River, 40 to 45 miles northeast of the type locality of the Mascall flora. The plant bearing tuffs in this area are lithologically identical to the Mascall sediments; here and immediately to the east they are interbedded with the Columbia River basalt, indicating that the sediments and lava are in part, at least, contemporaneous. Pardee & Hewett (1914) and Gilluly (1937) correlate the lacustrine and fluviatile deposits and interbedded lava in this area with the Mascall formation and the Columbia River basalt. They do not extend the name "Mascall," however, to the local development of these sediments.

Algae have been recovered from only one of the Blue Mountains plant localities (Austin). This occurs on the west side of the Sumpter Valley Railroad cut about a quarter of a mile south of the now abandoned Austin Railroad Station, U.S.G.S., Sumpter Valley Quadrangle, 1901 ed., Grant Co., Oregon.

Stinking Water Basin.—The Stinking



TEXT-FIG. 1—Localities of fossil algae.

Water Basin is located about 60 miles south of the John Day Valley. Here over an area of several miles, structural conditions in the underlying basalt have allowed preservation of a thick series of tuffaceous shales, which interfinger with the basalt below, and usually are separated by overlying flows from younger, lithologically similar sediments above. The plant fossils have come from the central part of the basin where the beds are almost horizontal or dip gently to the east.

Algae have been recovered from two localities in the Stinking Water Basin. Locality P4006 occurs on the west and southwest bank of a small tributary to Stinking Water Creek about 36 miles east of Burns, and some 5 miles south of U. S. Highway 20, Map 16, CCC Grazing Service, northeastern Harney Co., Oregon.

Sediments at a second site (Trapa locality, P4121), may be somewhat younger than those at P4006. The fossil plant horizon at P4121, which is about 5 miles to the northeast of P4006, lies stratigraphically higher in the section than the other, and is devoid of diagnostic megascopic plant remains. The microflora does not give precise indication of the age of the sediments and recent discovery of vertebrate remains nearby suggests that they may be as young as lower Pliocene (J. Arnold Shotwell, personal communication, 1956).

OCCURRENCE OF THE MICROSCOPIC FOSSIL ALGAE

PEDIASTRUM

Previous fossil records.—Although *Pediastrum* is widely reported from Pleistocene sediments (Faegri & Iversen, 1950; Cookson, 1953; Borge & Erdtman, 1954), records of its occurrence from the Tertiary are uncommon. Davis (1916) referred to *Pediastrum*, a cellular type of algal body from the Eocene Green River shale, but neither described nor figured the material. Bradley (1929b, 1931) believed the specimen to be more similar to *Coelastrum*, remarking (1929b, p. 424) that "the number of the cells, their size, and the general aspect are nearly enough like *C. verrucosum* to warrant the suggestion that the fossil may be a species of *Coelastrum* comparable to *C. verrucosum* Reinsch." Iversen (1936) mentioned recovery of *Pediastrum* colonies as secondary constituents from samples of boulder clay from Denmark. These specimens occurred with other microfossils and pollen of Tertiary and interglacial age. While none of them can be said to stem unquestionably from pre-Quaternary sediments, their association with Tertiary pollen suggests that some, at least, may also have been derived from older deposits. Erdtman (1936) briefly mentioned specimens of *Pediastrum* referred to *P. boryanum* (Borge & Erdtman, 1954) from the Headon beds (Oligocene or possibly Eocene) from the Isle of Wight. Wilson & Hoffmeister (1953) isolated abundant *Pediastrum* colonies from shale of probable Eocene age from Sumatra, from among which they described four new species, and Cookson (1953) has reported specimens of *P. boryanum* from carbonaceous shales of (?) early Tertiary age from South Australia and late Tertiary age from Victoria. I have also recovered colonies of *Pediastrum* cf. *P. boryanum* from the Florissant paper shales of Oligocene age (McGinitie, 1953) and specimens of the same morphologic type from the Pliocene Bidahochi formation of northeastern Arizona.

Oregon material.—At least two distinct species of *Pediastrum* have been isolated from Mascall (Riverbank) and Stinking Water Basin sediments (P4006, P4121); none have been recovered from Blue Mountains. The most abundant of these resembles *P. boryanum* (Turpin) Meneghini, a common green alga of essentially cosmopolitan distribution. The fossil specimens appear to be fully compatible morphologically with this living organism.

The colonies consist of uniseriate, nonperforated discs, usually more or less round in outline (pl. 64, figs. 5,6). The individual cells are polygonal, more or less regularly 4–6-sided, with the cell walls conspicuously marked. The marginal coenocytes are terminated to the exterior by two straight, roughly conical, blunt-tipped processes. The coenobia show considerable range in size (colonies from about 30 to 165 microns in diameter have been observed), and cell numbers. The determination of the exact number of cells is frequently difficult because the colonies are often incomplete and/or the cell walls have deteriorated. Colonies with 4, 8, and 16 coenocytes are figured together with the outline of a small marginal portion of one of the larger colonies for size comparison (text-fig. 2). The cell membrane of these specimens are smooth (pl. 64, fig. 6) or slightly warty (pl. 64, fig. 5).

Rarely occurring fossils in the Stinking Water and Trapa microfloras may be compared most closely with the living *P. duplex* Meyen (pl, 64, fig. 7; text-fig. 2f). Their coenobia also consist of a uniserate disc of coenocytes, but prominently perforated, with the central cell absent. Many of the colonies consist of 16 cells, although some with greater and smaller numbers have also been seen. The coenocytes are arranged in concentric rings, two in the 16-celled forms

to five or more in colonies with larger numbers of cells. The coenocytes are polygonal, 4–5-sided; those on the periphery terminate with bifurcating, blunt-tipped processes. On all specimens, the inside cells make either a single or a double point of contact with cells in the next outside ring. The coenocyte membrane is pitted or micro-reticulated among the former; it is smooth among those colonies with the latter configuration. The perforations, where neither collapsed, nor distorted, are slightly smaller than the individual inner coenocytes, but similar in shape to them. The colonies seen range from about 40 to 116. microns in diameter.

The fossil non-perforated colonies unquestionably resemble *P. boryanum*. Some workers comparing Tertiary specimens with this living alga, have accepted this morphologic similarity as indicating that the fossils and *P. boryanum* are conspecific. The similarity between the fossil perforated colonies, and *P. duplex*, is not, however, as conspicuous. On the one hand, *P. duplex* is the only species among these algae which always has a distinctly perforated colony and peripheral cells terminated exteriorly by two apically unthickened, non-bifurcating processes lying in the same plane—characteristics shared with the fossils. On the other hand, *P. duplex* (*typicum*) possesses a central cell, lens-shaped perforations, coenocytes which make two points of contact (their outer margin is concave) with the inner side of adjacent coenocytes, and a smooth cell membrane. This combination of characteristics does not occur among the fossil perforated forms. The 15–16 varieties of *P. duplex* described and illustrated (Raciborski, 1889; Brunnthaler, 1915) also differ from them in one or more of the following features: 1) presence of a central cell; 2) ornamentation of the cell wall; 3) geometry of the inner or the peripheral coenocytes. Thus there is at least some foundation for suggesting that the fossil material is morphologically distinct from *P. duplex*. Furthermore, among the perforated colonies there are differences in the pattern of the membrane wall, and in the nature of the contact between the coenocytes. Whether this morphologic diversity among the fossil specimens and the differences between them and the living species which they most resemble, are attributable to the variability of these organisms, or indicate more fundamental differences can only be conjectured. For while the form and simplicity of the *Pediastrum* coenobium clearly delimits it, the alga is extremely polymorphic. Specific distinction in living material is based primarily on the form of the central and peripheral cells, the perforation of the colony, and the ornamentation of the cell membrane (West & Fritsch, 1927, p. 113; Smith, 1933, p. 484). The alga is highly variable in these respects, however, as well as in cell number, proportion and arrangement; apparently few workers are able to agree as to the number, limits, and characterization of its species (Harper, 1916; West & Fritsch, 1927). As a result, many species and varieties of *Pediastrum* have been described which probably represent growth forms or "life cycle stages" and it seems reasonable to assume that such variability has always been characteristic of this group. While an unequivocal morphological resemblance between the fossil material and *P. duplex* is not indicated, it is impossible to refute the possibility of relationship between them.

Botryococcus

Previous fossil records.—Blackburn & Temperley (1936), Harris (1938), and Traverse (1955a) have reviewed the morphology and the geologic and geographic distribution of *Botryococcus*. Other Tertiary occurrences of this alga have been reported from the Eocene of India (Rao & Misra, 1949; Vimal 1953) and western Pakistan (Nagappa, 1957), the Oligocene of North America (Traverse, 1955a,b), the Miocene of Denmark (Ingwersen, 1954), the Pliocene of Germany (Straus, 1952), the early Tertiary to Pliocene of Australia (Cookson, 1953), the Tertiary of France (Fremy & Dangeard, 1938), and the Tertiary of Brazil (Dietz & Thiergart, 1957). Pre- and post-Tertiary records of *Botryococcus* are common from many parts of the world and it is generally believed that remains of this hydrocarbon producing alga are responsible for localized deposits of boghead coal in Alaska, Australia, France, Scotland, South America, and the United States.

Oregon material.—Fossil specimens of *Botryococcus* from the Mascall formation (Riverbank and Meadow localities), Blue Mountains and Stinking Water Basin (P4006, P4121) have been compared with illustrations and descriptions of fossil and living specimens of *Botryococcus braunii* Kützing and with individuals of this species recovered from Pleistocene sediments from the Channing Basin of northwestern Texas (pl. 64, figs. 3,4). The Miocene material appears morphologically identical to this common, cosmopolitan species.

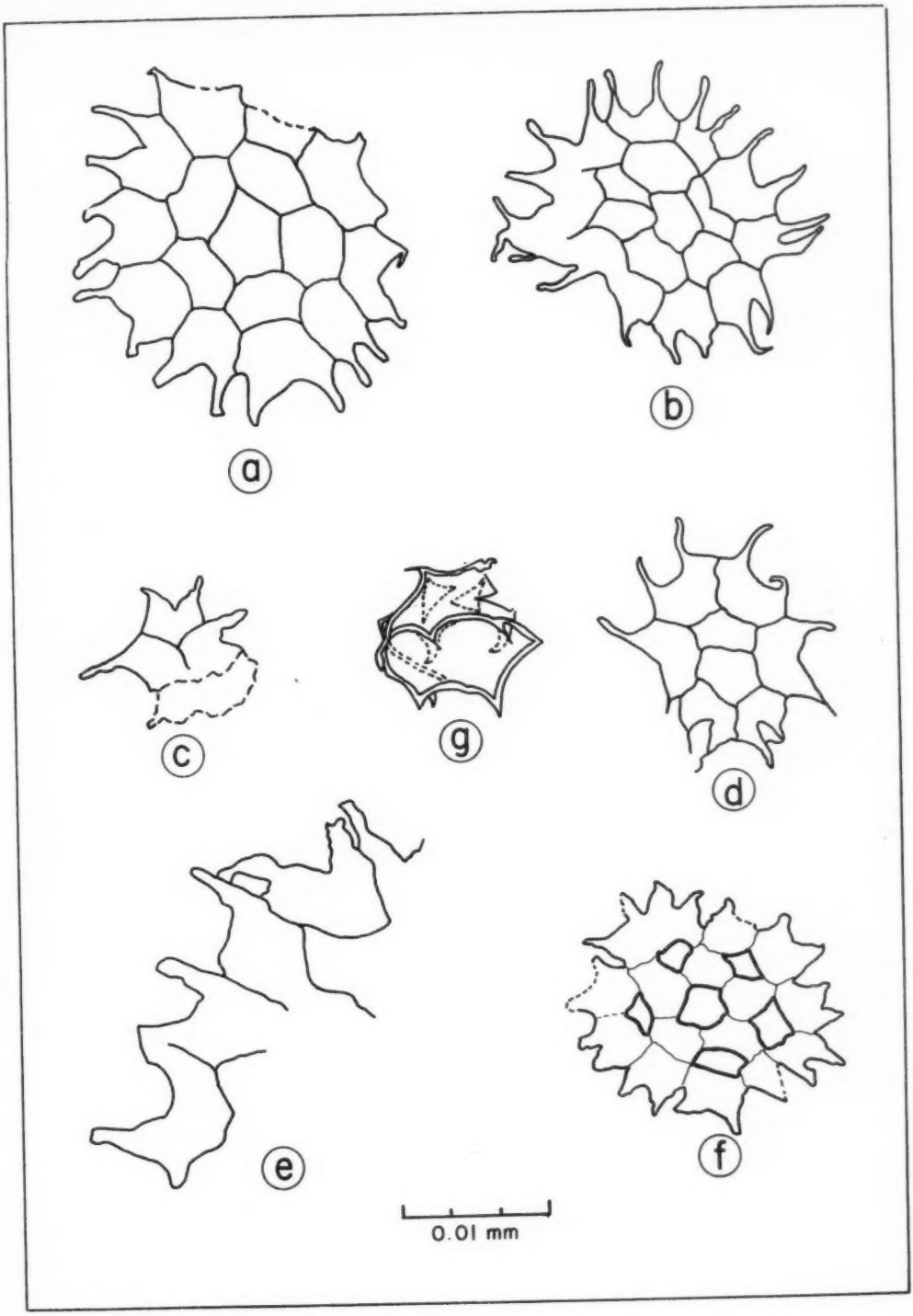
The complex morphology of the *Botryococcus* thallus was first understood as the result of researches of Blackburn & Temperley (1936). The colony is generally irregularly botryoidal in shape and in life composed of ellipsoidal or "pear-shaped" cells arranged radially in twos and fours as the result of dichotomous, longitudinal branching. In living condition, each pear-shaped cell sits immediately within a thin, cuticular and waxy structure—the thimble—which, in turn, is embedded in a thicker cup-like sheath of fatty material. A cell cap of pectic and cellulosic substances closed the cell chamber at the distal end. The whole is crowded together densely in a tough, dark, semi-opaque mass of mucilage which surrounds the entire colony. In the fossil forms illustrated only a "skeleton" remains, which consists (Temperley, p. 860) "of the most rigid part of the secreted framework of the colony . . . believed by Dr. Blackburn to represent the cuticularized layers." In some of the figured specimens the dichotomous, cup-like chambers are obvious (pl. 64, figs. 2–4). In many specimens, however, particularly among the larger thalli, disintegration of the thimble wall leaves only a general impression of these chambers, and the colonies often appear as more or less amorphous, botryoidal structures (pl. 64, fig. 1).

Tetraedron

Previous fossil records.—Bashnagel (1942) compared specimens from the Middle Devonian, Onondaga limestone of New York with four living species of *Tetraedron*. White (1862) had referred identical specimens from the Onondaga to the genus *Xanthidium*. The material recorded as *Xanthidium* by White, including the *Tetraedron*-like forms described by Bashnagel, are now recognized as members of the Hystrichosphaeridae, marine organisms of unknown affinity widely collected from rocks of Ordovician to Recent age. The *Tetraedron*-like forms of Bashnagel are referable to the genus *Hystrichosphaeridium* (Deflandre, 1944). Bradley (1929a, 1929b, 1931) figured a single specimen from the Green River formation, Colorado, which he compared with the living *T. regulare* var. *torsum* (Turner) Brunnthaler.

Oregon material.—Several rather poorly preserved complete specimens and occasional fragments in the Mascall (Meadow) and Stinking Water (P4006) microfloras, are similar to *Tetraedron*, although they cannot be matched with any of the living species. Morphologically, they seem most similar to members of either sections Polyedrium or Pseudostraurastrum of the genus *Tetraedron* (cf. Brunnthaler, 1915), and come closest to resembling *T. horridium* W. and G. S. West. Certain algae, however, such as *Pediastrum*, *Hydrodictyon*,and *Oocys-*

Text-fig. 2—Camera lucida drawings of fossil algae from the Mascall, Blue Mountains and Stinking Water microfloras; a–e, *Pediastrum* cf. *P. boryanum* Kützing. Specimens illustrating variation in size and cell number. a–d, complete or essentially complete colonies. a, Stinking Water, Oregon, specimen illustrated in pl. 64, fig. 5. b–d, Mascall, Oregon (Riverbank locality), drawn from glycerine slides. e, Small marginal portion of large colony, Stinking Water, Oregon (loc. P4121), drawn from glycerine slide. f, *Pediastrum* cf. *P. duplex?* Meyen. Stinking Water, Oregon (loc. P4006), drawn from glycerine slide. g, *Tetraedron?* sp. Mascall, Oregon (Meadow locality).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tis have *Tetraedron*-like stages in their life cycles (West, 1916; West & Fritsch, 1927; Smith, 1933). Unless reproduction by autospores can be demonstrated, there is no way of being certain that tetraedroid forms can be identified with *Tetraedron*. For this reason, and because of uncertain resemblance to any living species, the fossil specimens are only tentatively referred to this genus.

The solitary cells (text-fig. 2g) are polyhedric, with rounded angles produced into single, straight? spines. Some spines on the figured specimen are bent, but this probably occurred during preservation. The spines are various in size and length, ranging on the figured specimens from about 2.8 to 5.6 microns. The wall is thin, about .7 micron, and the membrane is smooth. The size of the figured specimen, including spines, is about 35 microns.

CONCLUDING REMARKS

Nomenclature.—Two families of chlorophycean algae, the Hydrodictyaceae, and the Botryococcaceae, are represented among the Miocene microfossils by specimens referred to *Pediastrum* and *Botryococcus*. A third family, the Oocystaceae, may be represented by specimens tentatively referred to *Tetraedron*. The morphologic similarity between fossil and living specimens of the former algae is so pronounced that there is no doubt of the generic references. In addition, some of these algae seem to be morphologically identical to the Recent species, *B. braunii* and *P. boryanum;* others are closely similar to *P. duplex*. None of the fossils have been identified with these species, although we appear to be dealing with organisms which show little or no morphologic variability throughout an extended geologic history. Of the algae herein discussed, only *Botryococcus* has at present, a pre-Tertiary record. Algae are known, however, from the Precambrian to the present. Certain families within the Chlorophyta are represented in the Paleozoic, and a number of forms closely resembling living genera are known from the Mesozoic. Moreover, these microscopic green algae are types which may be considered morphologically primitive, and an extended geologic history for them does not seem improbable. Following the example of Harris (1938) most workers have recorded the living species, *B. braunii*, from sediments from the Ordovician to the Recent.

Pre-Pleistocene occurrences of *Pediastrum* are essentially unknown. Cookson (1953) and Borge & Erdtman (1954) extended the range of *P. boryanum* into the Tertiary and possibly the early Tertiary. On the other hand, Wilson & Hoffmeister (1953) did not refer early Tertiary specimens of *Pediastrum* to the species which they resembled, *P. clathratum*, *P. simplex*, *P. boryanum*, and *P. duplex*, presumably adhering strictly to paleobotanical convention.

The identification of fossil algae with living species assumes that similarity in gross morphology is sufficient indication of relationship. Essentially all fossils are identified with, or related to living material on this premise. Morphology has played a pre-eminent part, however, in the classification of certain organisms. Fossil algae would appear less perfectly known than many fossil forms since they are classified primarily on pigmentation, metabolic products, methods of reproduction, features of the life cycle, and so on, none of which can be demonstrated among fossil specimens. On the one hand, the unfailing identification of fossil algae with living species on the basis of morphologic similarity alone, may leave the algologist with the same dilemma of which Steere (1946, p. 298) wrote when he remarked—"The greatest taxonomic problem confronting those who study fossil mosses and hepatics is a paradoxical one—instead of being lumped into form-genera, they have been 'identified' with a misleading precision and exactitude." On the other hand, the application of new species names to Tertiary and pre-Tertiary algae morphologically similar or identical to living species probably takes too great a cognizance of the age differences involved, fails to consider the nature of the organisms and the possibility of an extended geologic history, and may give significance to morphologic variability that is within the limits of a modern species.

Ecology and paleoecology.—Other than indicating the fresh-water origin of the sediments in which they occur, the presence of *Pediastrum*, *Botryococcus*, and *Tetraedron*

has little ecologic significance. Like many members of fresh-water algal floras, these genera are essentially cosmopolitan in distribution, living and thriving practically everywhere where there is light and moisture, in almost every available type of fresh-water habitat.

Pediastrum often occurs abundantly among the "aquatic macrophytes of the benthic region of pools and lakes" (West, 1916, p. 432) and almost always forms a part of the plankton in the same environments. It is an occasional part of the planktonic vegetation of slow or moderately slow rivers and "Isolated individuals . . . are often encountered in collections from permanent or semipermanent pools and ditches." (Smith, 1933, p. 484; West, 1916). At present, according to Prescott (personal communication, Nov. 17, 1955), published records do not indicate the occurrence of *Pediastrum* in Oregon, although he has found some or all of the following species, *P. duplex*, *P. boryanum*, and *P. tetras*, in coastal and high altitude ponds of the Wallowa Mountains and low altitude ponds of the Cascades, near Mt. Jefferson. Any restriction of its distribution in Oregon, however, is probably more apparent than real, for it seems likely that collections from the central part of the state would contain *Pediastrum*. *Botryococcus* usually occurs as a member of the fresh-water plankton in ponds and lakes (it may also be found "in ditches, bogs, tanks, water-butts," West & Fritsch, 1927, p. 304) and has been reported from brackish and salt water habitats in Russia (Blackburn & Temperley, 1936) and South Australia (Cookson, 1943). Many of the species of *Tetraedron* occur somewhat infrequently in small, stagnant waterbodies, although a few may be abundant among the fresh-water plankton (West, 1916, p. 200; West & Fritsch, 1927).

No attempt was made to obtain quantitative data on the number of thalli of *Pediastrum* or *Botryococcus* in any of the microfloras as it was difficult to determine with certainty when one was dealing with a complete colony, or only a broken or distorted fragment. Where it occurs, the imperforate P. *boryanum*-type is generally fairly common. The perforated colonies, on the other hand, are rare fossils. *Botyrococcus* is common in the Mascall and Stinking Water (P4006) microfloras; most abundant and best preserved at the Trapa locality; a rare constituent of the Blue Mountains microflora. Less than 6 specimens of *Tetraedron* were observed from the Mascall (Meadow) and Stinking Water (P4006) sediments. Drs. G. M. Smith (personal communication, Nov. 17, 1955) and G. W. Prescott (ibid.) have indicated that there is scarcely need to attempt explanations for variations in number of colonies of *Pediastrum* at the different localities where it occurs, and the same is probably true for the other algae. Prescott has suggested that the diversity in abundance of fossil specimens of this genus is probably quite "normal," because *Pediastrum* shows similar patterns in the aquatic flora today. Apparently, however, conditions which presently act to control divergence in absolute abundance among this alga are as yet undetermined. Nor, according to Prescott (Ibid), is there any "good correlation between colony morphology, wall decoration, and environmental conditions." Which might afford hints about their past surroundings and explain why they do not occur everywhere together in these Miocene lakes.

Most previously recorded fossil occurrences of *Botryococcus* have come from highly carbonaceous sediments (peats, lignites, carbonaceous clays, shales and sandstones) and it would appear that the conditions for the formation of botryococcoid deposits, or deposits rich in remains of this alga, may be rather specific (cf. discussion in Traverse, 1955a, pp. 345–346). *B. braunii* is so widely distributed at present, however, and, at least in this country, is so rarely abundant (Smith, 1933, p. 154) that it is unlikely that attempts to reconstruct the environment of deposition from its occurrence alone, can have much significance. It can be pointed out, however, that the most abundant and best preserved of the fossil *Botryococcus* colonies have come from the Trapa locality (P4121), so named because remains of the water-chestnut are the only abundant and common plant megafossil. This genus, native today to Asia and parts of Europe and Siberia, is naturally at home in rather small, shallow, often stagnant ponds and slow-running streams, an en-

vironment which apparently would also have favored most prolific growth of the alga *Botryococcus*.

BIBLIOGRAPHY

BASCHNAGEL, R. A., 1942, Some microfossils from the Onondaga chert of central New York: Buffalo Soc. Nat. Sci. Bull., v. 17, no. 3, p. 1–8.

BLACKBURN, K. B., & TEMPERLEY, B. N., 1936, *Botryococcus* and the algal coals: Part I, A reinvestigation of the alga *Botryococcus Braunii* Kutzing (by K. B. Blackburn): Part II, The boghead controversy and the morphology of the boghead algae (by B. N. Temperley): Royal Soc. Edinburgh Trans., v. 58, pt. 3, no. 29, p. 841–868.

BORGE, O., & ERDTMAN, GUNNER, 1954, On the occurrence of *Pediastrum* in Tertiary strata in the Isle of Wight: Botaniska Notiser, Heft 2, p. 112–113.

BRADLEY, W. H., 1929a, Neue Beobachtungen über Algen als Urmaterialien der Bogheadkohlen und schiefer: Centralbl. Mineralogie, Abt. B., p. 182–190.

——, 1929b, Fresh water algae from the Green River formation of Colorado: Torrey Bot. Club Bull., v. 56, p. 421–428.

——, 1931, Origin and microfossils of the oil shale of the Green River formation of Colorado and Utah: U.S.G.S. Prof. Paper 168, 58 p.

BRUNNTHALER, JOS., 1915, Protococcales, *in* Pascher, A., Die Süsswasserf. Deutschlands, Osterreichs. u. d. Schweiz: Heft 5, p. 52–205.

CHANEY, R. W., 1959, Miocene floras of the Columbia Plateau. Part I: Composition and Interpretation: Carnegie Inst. Wash. Pub. 617, p. 1–34.

COOKSON, I. C., 1953, Records of the occurrence of *Botryococcus braunii*, *Pediastrum* and the Hystrichosphaeridae in Cainozoic deposits of Australia: Nat. Mus. Melbourne Mem., no. 18, p. 107–123.

DAVIS, CHARLES, 1916, On the fossil algae of the petroleum-yielding shales of the Green River formation of Colorado and Utah: Nat. Acad. Sci. Proc., v. 2, no. 3, p. 114–119.

DEFLANDRE, GEORGES, 1944, Microfossiles des calcaires Siluriens de la Montagne Noire: Annales de paleontologie, tome XXXI, p. 41–75.

DIETZ, CURT, & THIERGART, FREDERICK, 1957, Der Marahunit, seine Verbreitung und stratigraphische Stellung im Tertiär am Rio Marahu im Staate Bahia (Brasilien): Beihefte zum Geologische Jahrbuch, Heft 25, p. 105–147.

DOWNS, THEODORE, 1956, The Mascall fauna from the Miocene of Oregon: Univ. of Calif. Publ. in Geol. Sci., v. 31, no. 5, p. 199–354, pls. 5–12, 50 text-figs.

ERDTMAN, GUNNER, 1936, New methods in pollen analysis: Svensk. bot. tidskr., Bd. 30, Heft 2, p. 154–164.

FAEGRI, KNUT, & IVERSEN, JOHS., 1950, Textbook of modern pollen analysis: Ejnar Munksgaard, Copenhagen, 168 p., 4 pls., 15 text-figs.

FREMY, P., & DANGEARD, L., 1938, Observations sur le *Botryococcus braunii* Kutzing actuel et fossile: Annales de paleontologie, v. 27, p. 117–136.

GRAY, JANE, 1956, Fossil green algae from the Miocene of the Columbia Plateau: Geol. Soc. Amer., Bull., v. 67, no. 12, pt. 2, p. 1768 [abstract].

——, 1958, Plant microfossils from the Miocene of the Columbia Plateau, Oregon: Ph.D. Dissertation, Univ. of Calif., Berkeley (unpublished).

GILLULY, JAMES, 1937, Geology and mineral resources of the Baker Quadrangle, Oregon: U.S.G.S., Bull. 879, 119 p., 3 pls., 7 text-figs.

HARPER, R. A., 1916, On the nature of types of Pediastrum: New York Bot. Garden Mem., v. 6, p. 91–104.

HARRIS, T. M., 1938, The British Rhaetic flora: British Museum (Nat. History), London, p. 9–80.

INGWERSEN, PETER, 1954, Some microfossils from Danish late-Tertiary lignites: Danm. geol. Unders., II Raekke, Nr. 80, p. 32–64.

IVERSEN, JOHS., 1936, Sekundärer Pollen als Fehlerquelle: Danm. geol. Unders., IV Raekke, Bd. 2, Nr. 15, 24 p.

MACGINITIE, H. D., 1953, Fossil plants of the Florissant beds, Colorado: Carnegie Inst. Washington, Pub. 599, 198 p., 75 pls., 1 text-fig.

MERRIAM, J. C., 1901, A contribution to the geology of the John Day Basin: Univ. of Calif. Publ., Bull. Dept. Geology, v. 2, no. 9, p. 269–314, 2 figs.

——, & SINCLAIR, W. J., 1907, Tertiary faunas of the John Day region: *Ibid.*, v. 5, p. 171–205.

NAGAPPA YEDATORE, 1957, Further occurrences of *Botryococcus* in western Pakistan: Micropaleontology, v. 3, no. 1, p. 83.

PARDEE, J. T., & HEWETT, D. F., 1914, Geology and mineral resources of the Sumpter Quadrangle, Oregon: Mineral resources of Oregon, Oreg. Bur. Mines and Geol., v. 1, no. 6, p. 3–128.

RACIBORSKI, M., 1889, Przeglad Gatunkow Rodzaju Pediastrum: Rozpr. i. Sprawozd, Wydz. III, Akad. Umiej. w. Krakowie, tom. XX, p. 1–37.

RAO, S. R. N., & MISRA, S. S., 1949, An oil-bearing alga from the Palana lignite (?Eocene) of Rajputana: Current Sci., v. 18, no. 10, p. 380–381.

SMITH, G. M., 1933, The fresh-water algae of the United States: McGraw-Hill, New York, 716 p.

STEERE, W. C., 1946, Cenzoic and Mesozoic Bryophytes of North America: Amer. Midl. Nat., v. 36, no. 2, p. 298–324.

STRAUS, ADOLPH, 1952, Thallophyten, Kryptogramen und Gymnospermen aus dem Pliozan von Willershausen: Deutsche Bot. Gesell. Ber., Bd. LXV, Heft 4, p. 74–79.

THAYER, T. P., & HAY, R. L., 1950, Preliminary notes on later Miocene volcanism in the John Day region, Oregon: Northwest Sci., v. 24, p. 89–90.

TRAVERSE, ALFRED, 1955a, Occurrence of the oil-bearing alga Botryococcus in lignites and

other Tertiary sediments: Micropaleontology, v. 1, no. 4, p. 343–350.
——, 1955b, Pollen analysis of the Brandon lignite of Vermont: Bureau of Mines, Rept. of Invest. 5151, 107 p.
VIMAL, J. P., 1953, Occurrence of *Botryococcus* in Eocene lignites of Cutch: Current Sci., v. 22, p. 375–376.
WEST, G. S., 1916, Algae: v. I, Cambridge Botanical Handbooks, 475 p.
——, & FRITSCH, F. E., 1927, A treatise on the British freshwater algae: Cambridge University Press, London, 534 p.
WHITE, M. C., 1862, Discovery of microscopic organisms in the siliceous nodules of the Paleozoic rocks of New York: Am. Jour. Sci., 2nd ser., v. 33, p. 385–386.
WILSON, L. R., & HOFFMEISTER, W. S., 1953, Four new species of fossil *Pediastrum:* Am. Jour. Sci., v. 251, p. 753–760.

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JOURNAL OF PALEONTOLOGY, V. 34, NO. 3, P. 464–466, PL. 65, 2 TEXT-FIGS., MAY, 1960

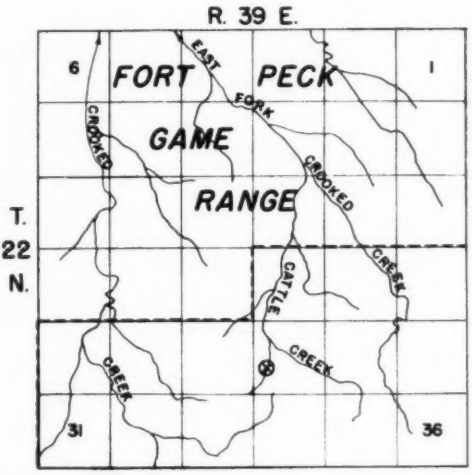
ON THE OCCURRENCE OF *EDMONTOSAURUS* IN THE HELL CREEK FORMATION OF MONTANA[1]

W. L. ROHRER AND R. KONIZESKI
United States Geological Survey

ABSTRACT—A specimen of *Edmontosaurus* from the Hell Creek formation of Montana substantiates the correlation of the Upper Cretaceous Hell Creek formation with the Upper Edmonton member of Alberta. It may be a new species.

INTRODUCTION

ON SEPTEMBER 1957, W. L. Rohrer collected a specimen of *Edmontosaurus* which apparently is specifically distinct from *E. regalis* (Lambe, 1917, p. 65). The specimen was found, in situ, about 38 feet above the contact between the Cretaceous Hell Creek and Fox Hills formations on Cattle Creek in the E½NW¼SW¼ sec. 27, T. 22 N., R. 39 E., Garfield County, Montana (see text-fig. 1). The specimen is a left dentary and was located in a concretionary sandstone and limestone mass at the junction of a forked lens of conglomerate, consisting of quartzite cobbles and ironstone nodules, near the base of a vertical cliff of sandstone in the Hell Creek formation (see text-fig. 2 for stratigraphic positions of formations).



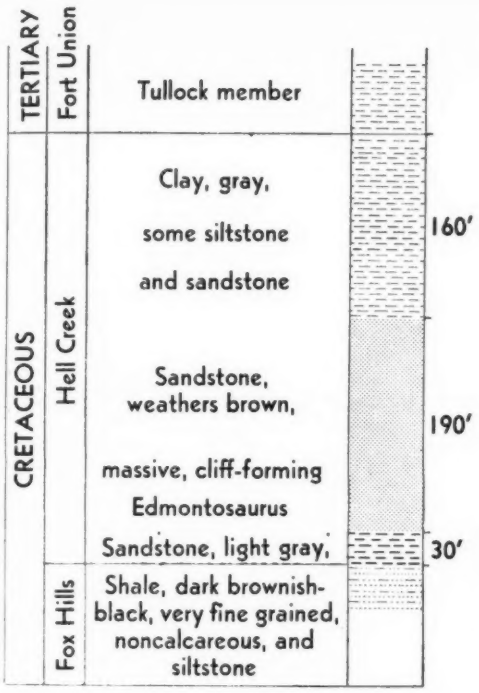
TEXT-FIG. 1—Map of part of Garfield County, Montana, showing fossil locality (encircled ×).

STRATIGRAPHY

The Fox Hills strata are conformable and transitional with the underlying marine Bearpaw shale and were " . . . found to be about 40 feet thick at the Cook ranch on Crooked Creek . . . " (Brown, 1907, p. 827). The formation is overlain by 380 feet of Hell Creek sediments on Cattle Creek. On Hell Creek, Brown (1907, p. 827), recorded about 80 feet of Fox Hills strata. The Fox Hills sandstone is light gray, very fine grained, friable, noncalcareous and is interbedded with light gray, noncalcareous siltstone.

The thickness of the uppermost Cretaceous formation in this area, the Hell Creek, is related to the thickness of the underlying, locally eroded, Fox Hills formation. The erosional unconformity at the top of the Fox Hills is a channeling of a broad nature, i.e., undulating rather than sharply incised. The inference is that the Fox Hills sediments were located in an area of low topographic relief upon which sluggish drainage developed and that they were not indurated before they were covered by the continental Hell Creek strata. This inference is more or less in agreement with previous workers in this area. Dobbin & Reeside (1929, p. 17) noted this relationship as follows: " . . . no evidence was found to indicate a major break at the top of the Fox Hills." A few small conglomerate lenses are scattered throughout the Hell Creek sandstone interval. These are composed of quartzite, ferruginous limestone, ironstone pebbles and cobbles, and occasional bone fragments. Such sporadic occurrences can only represent brief spate in surrounding

[1] Publication authorized by the Director, United States Geological Survey.



TEXT-FIG. 2—Stratigraphic section at fossil locality, Garfield County, Montana.

areas. Thus, as observed by Dobbin & Reeside (1929, p. 17), the presence of conglomerate affords little proof of the existence of a major unconformity at the Fox Hills and Hell Creek formational contact.

The basal Hell Creek formation stratigraphic section on Cattle Creek consists of approximately 30 feet of dark gray, carbonaceous shale with streaks of ironstone nodules and quartzite pebbles overlying the light gray sandstones and siltstones of the Fox Hills formation. The basal Hell Creek shale is in turn overlain by 190 feet of massive cliff-forming sandstone weathering rusty brown. The sandstone is medium to coarse grained and calcareous, containing occasional limestone concretions and less frequent lenses of conglomerate. The uppermost Hell Creek unit in this area is primarily clay, about 160 feet thick, with some siltstone and interbedded sandstone. This formation is overlain conformably by the Tullock member of the Fort Union formation. The Tullock-Hell Creek contact is at the base of the lowest lignite bed, which in this area is quite persistent and averages about 4 feet thick.

DESCRIPTION

At present the genus *Edmontosaurus* includes only one species, *E. regalis* Lambe (1917, p. 65). The holotype and several described specimens were all collected from the lower and middle members of the Edmonton formation in Alberta (Lull, 1942, p. 17; Sternberg, 1947, p. 5) which are stratigraphically equivalent to the Fox Hills sandstone of Montana (Billings Geological Society, 1953). On the basis of veretebrate fossils Sternberg (1947, p. 2) states that the upper member of the Edmonton formation is of Lance age; and Russell (1953, p. 95) correlates the upper member with the Hell Creek formation of Montana. Because *E. regalis* apparently did not continue across the very pronounced faunal break between the middle and upper members of the Edmonton formation (Sternberg, 1947, p. 4), and because it is unknown outside of Alberta, it is of considerable interest that a specimen of that genus has been collected in Montana from the upper Edmonton equivalent (Hell Creek formation). It is of further interest that the specimen is probably specifically distinct from *E. regalis*.

The holotype of *E. regalis* consists of a "Complete skull, most of the vertebrae in place back to the sixth caudal, one hind limb, lacking a phalanges, one humerus, both pubic bones, one ischium, the greater part of a right ilium, and some ribs" (Lambe, 1917, p. 65). In contrast to the relatively complete nature of the holotype, the Montana Hell Creek specimen consists of only a left dentary lacking the upper part of the coronoid process and a number of teeth (see plate 65 for lingual, crown, and labial views). Numerous differences exist between it and the described specimens of *E. regalis* (Table 1). However, because it represents such a small part of the animal's anatomy the dissimilarities are not necessarily specific but may be sexual and (or) due to individual variation. For this reason the Hell Creek specimen will not be described as a new species unless additional, substantiative material is collected. Considering the remarkable preservation of the specimen and the relative size and weight difference of it

TABLE 1—MEASUREMENTS OF TWO SPECIMENS OF *Edmontosaurus*

Item	Paratype[1] No. 2289	Cattle Creek Specimen USNM No. 22102
Breadth of cutting surface of teeth at its middle length	30 mm.	35 mm.
Vertical rows of teeth	48–49	54
Number of teeth in dentary	230	245
Average length of individual tooth from middle of series	30.5 mm.	36 mm.
Average width of individual tooth from middle of series	10.0 mm.	10.5 mm.
Length of dentary	about 780 mm.	730 mm.
Distance of inner cutting surface of teeth at mid-length of magazine, about lower border	190 mm.	195 mm.
Depth of bone just in advance of first vertical series of teeth	150 mm.	130 mm.
Length of dental magazine at its mid-height	366 mm.	410 mm.
Posterior depth of magazine	about 60 mm.	60 ± 5 mm.
Anterior depth of magazine	84 mm.	85 ± 5 mm.
Depth of magazine at its mid-length	145 mm.	145 mm.

[1] Measurements from Lambe, 1920, p. 40–41.

and the conglomerate cobbles of the bank in which it occurred there is little likelihood that there was transportation by stream action. Regardless of its specific affinities, the specimen has the two-fold value of substantiating the correlation of the Upper Cretaceous Hell Creek formation with the Upper Edmonton member, and shows that the ornithischian dinosaur, *Edmontosaurus*, survived into latest Cretaceous time.

REFERENCES CITED

Billings Geological Society, 1953, Correlation chart—Montana and adjacent areas in Guidebook, 4th annual field conference, 1953: Billings, Montana, p. 14.

BROWN, BARNUM, 1907, The Hell Creek beds of the Upper Cretaceous of Montana: Am. Mus. Nat. History, Bull. 23, p. 823–45.

DOBBIN, C. E., & REESIDE, J. B., JR., 1929, The contact of the Fox Hills and Lance Formations: USGS, Prof. Paper 158, p. 9–25.

LAMBE, L. M., 1917, A new genus and species of crestless hadrosaur from the Edmonton Formation of Red Deer Valley, Alberta: Ottawa Naturalist, v. 31, p. 65–73.

——, 1920, The hadrosaur *Edmontosaurus* from the Upper Cretaceous of Alberta: Canadian Geol. Survey, Mem. 120 (Geological Series 102), p. i–ii, 1–79.

LULL, R. S., & WRIGHT, N. W., 1942, Hadrosaurian dinosaurs of North America: Geol. Soc. Am. Spec. Paper 40, p. 1–242.

RUSSELL, L. S., 1953, Upper Cretaceous stratigraphy of southern Saskatchewan: Billings Geol. Soc. Guidebook, 4th annual field conference, p. 87–101.

STERNBERG, C. M., 1947, The upper part of the Edmonton Formation of Red Deer Valley, Alberta: Canadian Dept. Mines and Resources, Mines and Geology Branch, Geol. Survey Paper 47-1, p. 1–11.

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EXPLANATION OF PLATE 65

FIGS. *1–3*—*Edmontosaurus* sp., lingual, crown, and labial views. USNM No. 22102; from Cattle Creek, Garfield County, Montana; Upper Cretaceous Hell Creek formation. Photographs courtesy of Smithsonian Institution.

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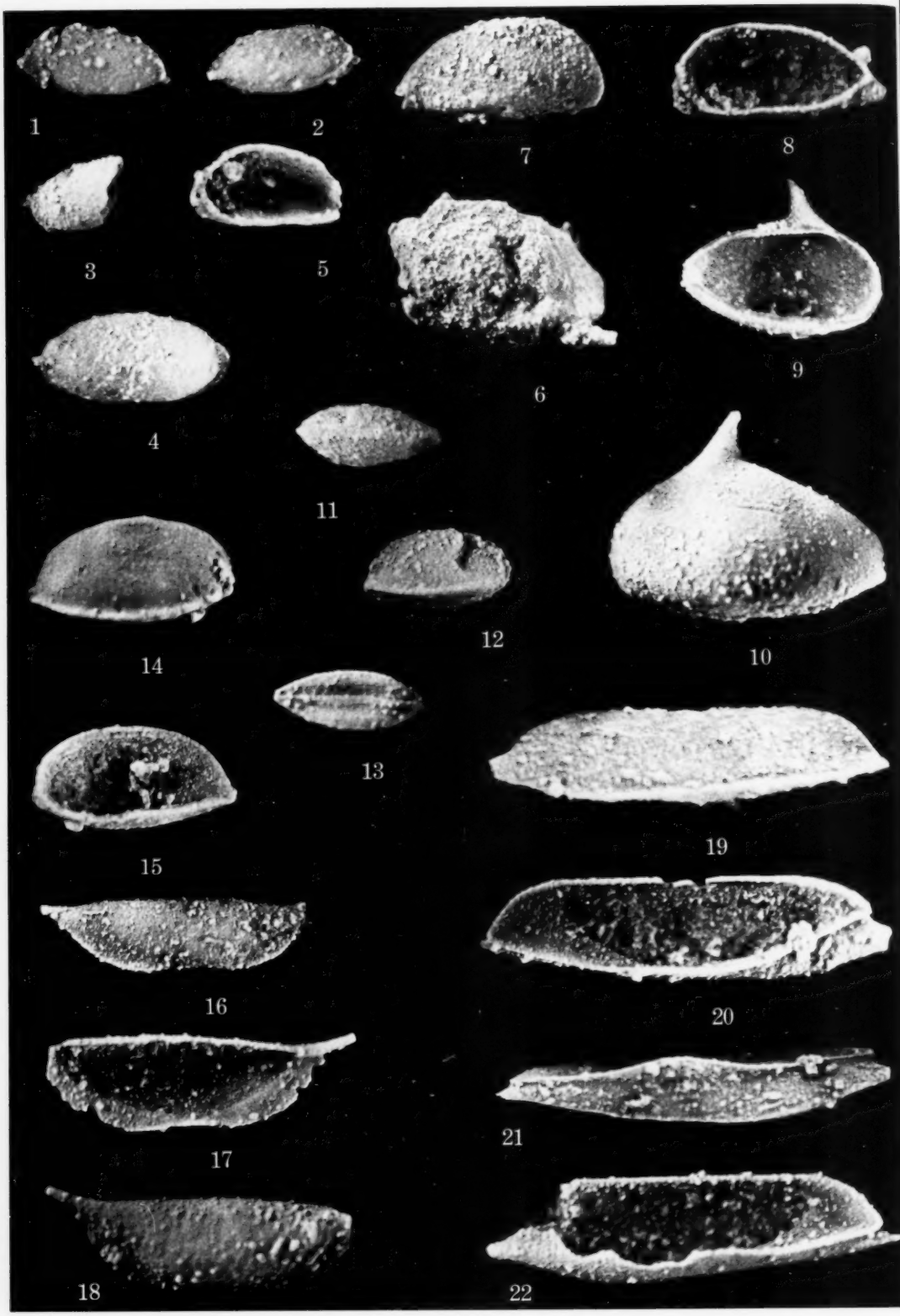
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JOURNAL OF PALEONTOLOGY, V. 34, NO. 3, P. 467–478, PL. 66, MAY, 1960

REVISION OF THE OSTRACODE FAMILY BEECHERELLIDAE AND REDESCRIPTION OF ULRICH'S TYPES OF *BEECHERELLA*[1]

JEAN M. BERDAN
U. S. Geological Survey, Washington, D. C.

ABSTRACT—Restudy of the types of the species assigned to *Beecherella* by Ulrich in 1891 shows that the family Beecherellidae, consisting of the genera *Beecherella* and *Acanthoscapha*, belongs in the Podocopa. *Acanthoscapha* Ulrich & Bassler 1923 is a senior synonym of *Alanella* Bouček 1936. Most of the species originally assigned to *Beecherella* belong in various other genera and families.

INTRODUCTION

THE types of several species and genera included in the family Beecherellidae have been examined during preparation of a section on this family for Volume Q (Ostracoda) of the Treatise on Invertebrate Paleontology, R. C. Moore, editor. Since some of the taxonomic changes made in the Treatise may seem arbitrary, this paper is presented to document certain revisions.

The genus *Beecherella* was described by Ulrich (1891, p. 197–204), who assigned to it 6 species and 1 variety. Subsequently Ulrich (1894, p. 691, 692) proposed the family Beecherellidae, to include the genera *Beecherella* Ulrich, 1891, and *Krausella* Ulrich, 1894, and suggested that *Beecherella* be restricted to the type species only. The genus *Acanthoscapha* was added to the family by Ulrich & Bassler (1923, p. 318, 319). Bassler & Kellett (1934, p. 145, 184) transferred all the species originally described as *Beecherella*, with the exception of the type species, to *Acanthoscapha*.

The 6 species and 1 variety described by Ulrich in 1891 are as follows: *Beecherella carinata*, the type species of *Beecherella; B. subtumida; B. subtumida* var. *intermedia; B. ovata; B. cristata; B. navicula*, the type species of *Acanthoscapha* Ulrich & Bassler; and *B. angularis*. Of the seven taxa, the type

[1] Publication authorized by the Director, U. S. Geological Survey.

EXPLANATION OF PLATE 66

FIGS. *1–4*—"*Beecherella*" *cristata* Ulrich. *1,2*, right lateral and left lateral views of complete carapace of topotype, YPM 20840, ×23, *3*, left view of holotype, USNM 41816, ×24, *4*, right valve of paratype, USNM 41816, ×23.

5—"*Beecherella*" *subtumida* var. *intermedia* Ulrich, internal view of holotype, USNM 41818, ×25.

6—"*Beecherella*" *ovata* Ulrich, left view of holotype, YPM 20394, ×24.

7–10—*Janusella subtumida* (Ulrich). *7*, lateral view of right valve, paratype, USNM 41817, ×23, *8*, lateral view of interior of right valve, lectotype, YPM 20395, ×24, *9*, lateral view of interior of left valve, topotype, YPM 20841, ×23, *10*, lateral view of left valve, topotype, YPM 20842, ×23.

11–15—"*Beecherella*" *angularis* Ulrich. *11–13*, dorsal, right lateral and ventral views of complete carapace, topotype, YPM 20843, ×23. Note that depression on anterodorsal portion of *12* is due to poor preservation and is not a shell feature. *14–15*, lateral and interior views of holotype, right valve, YPM 20397, ×23.

16–18—*Acanthoscapha navicula* (Ulrich). *16*, left view of a complete carapace, topotype, YPM 20844, ×24, *17*, internal view of lectotype left valve, YPM 20390, ×23, showing duplicature, *18*, external view of lectotype, ×23.

19–22—*Beecherella carinata* Ulrich. *19–21*, lateral exterior, lateral interior and ventral views of right valve, holotype, YPM 20392, ×23. Note that *20* shows duplicature. *22*, interior view of left valve, topotype, YPM 20845, ×23, showing duplicature.

specimens of four are broken, two of them, *B. subtumida* var. *intermedia* and *B. ovata*, in such a way that the species are unrecognizable. The type of *Beecherella navicula* was apparently broken at the time Ulrich described it, although this is not mentioned in his description. The type of *Beecherella cristata* was broken after being described and illustrated, but can be identified with topotype specimens. The types of the three remaining taxa, *B. carinata*, *B. subtumida* and *B. angularis*, are relatively well preserved. They show structures indicating that the last two belong to genera other than *Beecherella*. Consequently it has seemed desirable to redescribe the types of all of Ulrich's species, and to redefine the Beecherellidae in the light of current knowledge.

According to Ulrich (1891, p. 197), the specimens he studied were sent to him by C. E. Beecher and Charles Schuchert. Apparently all came from a collection of silicified material which Beecher was etching with hydrochloric acid. The types sent by Beecher were returned to him, and are now in the collection of the Yale Peabody Museum, but those sent by Schuchert were retained by Ulrich and are now in the collections of the U. S. National Museum. Statigraphic and locality data listed on the labels of the types are "Lower Helderberg group, Albany County, N. Y.," as is published in the original descriptions, but labels on the unpicked fine material in Beecher's collection at Yale read "Lower Helderberg group, Indian Ladder, N. Y." According to Dr. Winifred Goldring (oral communication) Beecher made his collections from a stone wall around a field near Indian Ladder. Although this makes the stratigraphic position of the material ambiguous, the presence of many specimens of *Dicaelosia varica* (Conrad) associated with the ostracodes suggests strongly that the rocks came from the Kalkberg limestone, as according to Dr. Lawrence V. Rickard and Dr. Donald W. Fisher (oral communication) this brachiopod is limited to the Kalkberg limestone in eastern New York.

Beecher's collection contains a rich fauna which has been only partially described. Beecher (1893) himself described some of the trilobite protaspides, since restudied by Whittington (1956a, b). Some of the sponges described by Girty (1895) also came from this collection. The Bryozoa, which are exceedingly abundant, have been mentioned but never adequately treated, and the Brachiopoda, which mostly belong to described species, have never been listed. The ostracode faunule is diversified. Ulrich (1891, p. 198), in commenting on the rarity of *Beecherella*, lists as other more abundant forms two species of *Aechmina*, and also "*Beyrichia*, *Kloedenia*, *Bollia*(?), *Moorea*, *Bythocypris*, etc." In addition to *Beecherella* and *Acanthoscapha*, species of the following genera are present in the samples that I have examined: *Aechmina* Jones and Holl 1869; *?Aechminaria* Coryell & Williamson 1936; *Placentella* cf. *P. elliptica* Wilson 1935; *Bollia* Jones & Holl 1886; *Ulrichia* Jones 1890; *Kirkbyella* Coryell & Booth 1933; *Parabolbina* Swartz 1936; *Velibeyrichia* Henningsmoen 1954; *Saccarchites* Swartz & Whitmore 1956; *?Octonaria* Jones 1887; *?Thlipsurella* Swartz 1932; *Janusella* Roth 1929; *Tricornina* Bouček 1936; *Berounella* Bouček 1936; *Tubulibairdia* Swartz 1936; as well as several undescribed genera. This is an important and interesting fauna, but because the collection was made from float, and stratigraphic and geographic data are inadequate, it seems advisable to postpone its study until the faunule can be found in place.

Prof. Carl O. Dunbar and Dr. Karl M. Waagé of the Yale Peabody Museum, and Dr. G. A. Cooper of the U. S. National Museum, kindly permitted me to borrow the types on which this study is based. The paper has been greatly improved by a number of stimulating discussions with my colleague, I. G. Sohn. Photographs were taken by Anita Epstein and Marcia Newell.

SYSTEMATIC DESCRIPTION

Family BEECHERELLIDAE Ulrich 1894

Long, smooth, slightly asymmetrical ostracodes with long, adont hinge parallel to the ventral margin and with spines on anterior and posterior ends of one or both valves. Duplicature present, muscle scar unknown.

Stratigraphic range.—Upper Silurian to Middle Devonian, Mississippian(?).

Discussion.—In his description of *Bee-*

cherella carinata, Ulrich (1891, p. 200), mentioned a "thin, oblique, diaphragm-like structure" in the right valve, and indicated that he was uncertain whether or not this structure was a part of the shell, or an accident of preservation. He stated that it was absent in the "left" valve which he had examined. Out of ten additional right and left valves of *B. carinata* from Beecher's collection, six are well enough preserved to show this structure. There is little question that it represents a duplicature. A similar structure is present in the holotype and topotype specimens of *Acanthoscapha navicula*, the type species of *Acanthoscapha*. Consequently, these two genera are grouped together in the family Beecherellidae, and classed under the order Podocopa.

Kesling & Sohn (1958) have described the occurrence of a duplicature in their new species *Alanella devonica*, and by inference it should also occur in *Alanella bohemica* Bouček, the type of the genus. They suggest (*ibid.*, p. 518) the possibility that the family Alanellidae Bouček 1936 is a junior synonym of Beecherellidae Ulrich 1894. As the type of *Acanthoscapha navicula* is congeneric with *Alanella bohemica*, the genus *Alanella* is here considered a junior subjective synonym of *Acanthoscapha*, and the family Alanellidae, a junior synonym of the family Beecherellidae. As here revised, the Beecherellidae contains certainly two genera, *Beecherella* and *Acanthoscapha*, both of which are forms with relatively long, straight hingelines and demonstrable duplicatures. A third genus, *Ulrichella* Bouček 1936, is only questionably assigned to this family pending further study.

The family Alanellidae as originally proposed by Bouček (1936, p. 71) contained only *Alanella*, although in the same paper (*ibid.*, p. 72–73) he cited two genera, *Krausella* and *Ulrichella*, in the Beecherellidae. Henningsmoen (1953, p. 247, 273) questioned the position of the Alanellidae in the Paleocopa, and listed the following genera in the family: *Alanella* Bouček 1936, *Vltavina* Bouček 1936, *Berounella* Bouček 1936, *Tricornina* Bouček 1936, ?*Boucekites* Přibyl 1953, ?*Pribylites* Pokorný 1950, and ?*Pribylites* (*Parapribylites*) Pokorný 1950. He apparently did not consider the Beecherellidae as Paleocopa, as the family is not mentioned in his paper. Přibyl (1954, p. 102) followed Henningsmoen in placing *Tricornina* and *Boucekites* provisionally in the Alanellidae.

Most recently Mertens (1958, Table 7), in his tabular summary of the Ostracoda, has listed five genera in the Alanellidae. These are *Alanella*, *Berounella*, *Boucekites*, *Pribylites* and *Parapribylites*. This list resembles Henningsmoen's except for the omission of *Tricornina* and *Vltavina*. With the exception of *Alanella* (= *Acanthoscapha*), none of these genera can be transferred unquestionably to the Beecherellidae as redefined. *Pribylites* and *Parapribylites* probably belong in the Aparchitidae as originally stated by Pokorný (1950, p. 590). *Tricornina* and *Boucekites* differ from the beecherellids in having a relatively short hinge, and *Tricornina* lacks a duplicature. *Berounella* and *Vltavina* are sulcate, although the sulcus of the latter is weak.

Mertens (1958, Table 9) lists seven genera which have been assigned to the Beecherellidae. These are: *Beecherella* Ulrich 1891, *Acanthoscapha* Ulrich & Bassler 1923; *Janusella* Roth 1929; *Rayella* Teichert 1939; *Steusloffina* Teichert 1937; *Ulrichella* Bouček 1936; and *Morrisitina* Gibson 1955. Of these seven genera, *Janusella*, *Rayella*, and *Steusloffina* lack the distinguishing characters of the family as redefined, and should be excluded. The systematic position of *Ulrichella* cannot be determined without further study. Until it can be established that this genus possesses a duplicature, it is only questionably included in the Beecherellidae, especially since according to the original description (Bouček, 1936, p. 73) it has two constrictions in the carapace. The holotype of the type species of *Morrisitina*, *M. gibbosa* Gibson, has been examined, and found to be a somewhat corroded complete carapace. Additional work will be necessary before the genus can be correctly assigned, but it is probable that it belongs with *Bairdia* rather than *Beecherella*.

Genus BEECHERELLA Ulrich, 1891

Beecherella Ulrich, 1891, p. 198–199; Ulrich & Bassler, 1923, p. 318–319; Bassler & Kellett, 1934, p. 38.

Type species.—By original designation, *Beecherella carinata* Ulrich, 1891, p. 199–

200, pl. II, figs. 1–4, Lower Devonian, (Helderbergian), Albany County, N. Y.

Diagnosis.—Smooth, elongate beecherellid ostracodes with flat venter and subtriangular cross-section. A short subconical spine is directed anteriorly and posteriorly on each valve.

Discussion.—Ulrich (1891, p. 198–199, pl. II, figs. 1-3) originally oriented this genus with the curved margin in lateral view considered as dorsal, and the larger spine anterior. Ulrich & Bassler (1923, p. 318, text-fig. 24, fig. 1), following Ulrich's (1894, p. 691) later suggestion, reversed the orientation of the original illustration so that the more strongly curved margin is shown as ventral, and described the larger spine as posterior. The orientation used in this paper follows that of Ulrich & Bassler, which agrees with the criteria proposed by Triebel (1941). Thus the orientation in Ulrich's original paper is reversed 180 degrees.

As previously mentioned, of the seven forms originally assigned to *Beecherella* by Ulrich, all but the type species have been placed in other genera. This is implied by Ulrich & Bassler (1923, p. 319), who cite *Beecherella carinata* as the "Genotype and only species" although, with the exception of *Acanthoscapha navicula*, these authors did not indicate the position of the other species. Bassler and Kellett (1934, p. 145, 184), however, list the remaining six forms under *Acanthoscapha*. Since 1934, two other species have been assigned to *Beecherella*, *B. bloomfieldensis* Swartz & Swain 1941, and *B. trapezoides* Gibson 1955. Neither of these species belong in *Beecherella* as redefined above. "*Beecherella*" *bloomfieldensis* is known only from internal casts and external molds, and there is no evidence from the description and illustrations (Swartz & Swain, 1941, p. 444–445, pl. 8, fig. 9g,9h) of any structure resembling a duplicature. Swain (1953, p. 279–280) states that this species should be referred to his new genus *Camdenidea*. "*Beecherella*" *trapezoides* lacks the discrete terminal spines of *Beecherella* as redefined, and, to judge from the holotype, is a bairdiid. The genus *Beecherella* is thus reduced once more to *Beecherella carinata* as the only species, but it is to be expected that other species will be found as more ostracode faunas become known from rocks of Lower Devonian age.

BEECHERELLA CARINATA Ulrich 1891
Pl. 66, figs. 19–22

Beecherella carinata Ulrich, 1891, p. 199–200, pl. II, figs. 1–4; Ulrich & Bassler, 1923, p. 318–319, text-fig. 24, fig. 1; Bassler & Kellett, 1934, p. 38, text-fig. 17, fig. 1.

Diagnosis.—Beecherellid with a ventral carina extending from the short anterior spine to the short, stout, hollow posterior spine on each valve.

Description of types.—A slide in the collections of the Yale Peabody Museum containing two specimens, YPM 20392 and YPM 20393, is labelled "*Beecherella carinata* Ulrich, types gen. et sp." These are the two specimens figured by Ulrich (1891, pl. II, figs. 1–4), the larger being represented by figs. 1–3, and the smaller by fig. 4. The larger, YPM 20392, is the specimen described on p. 199 and is here designated the lectotype of the species. The lectotype is a right valve, 2.85 mm. long and 0.65 mm. high. The width of the venter is 0.46 mm. A distinct carina extends from the anterior spine to the broken posterior spine. The dorsal margin is about 2 mm. long, and is straight and subparallel to the ventral margin. With the exception of the carina, the surface is smooth, although fragments of adventitious silica give it a rough appearance in the illustration (pl. 66, figs. 19–21). The interior has a well developed duplicature at the anterior end of the shell; the duplicature at the posterior end is less well developed and is partially obscured by adventitious silica. The valve has two notches where the shell was broken near the middle of the hinge line. The antero-dorsal margin is deflected ventrally at an angle of about 45 degrees to the hinge line; the postero-dorsal margin is less sharply deflected. In an interior view the ventral contact margin can be seen to swing upward posteriorly, and the posterior spine projects postero-ventrally behind it. The posterior spine is hollow.

Discussion.—Ulrich apparently based his description of the species only on the two specimens on the type slide, as no others are illustrated or mentioned in the text. How-

ever, the small specimen, YPM 20393, which he illustrated as "Interior view of a small left valve" (Ulrich, 1891, p. 204), shows the compressed ventroterminal areas of *Acanthoscapha*, and is probably a young instar of *Acanthoscapha navicula*. As previously mentioned, ten additional valves of *B. carinata* have been found in Beecher's collection, including four left valves. These show that the valves are nearly symmetrical, although the posterior spine is relatively smaller on the left valve. The ventral carina is present on both. The duplicature is not invariably preserved, but can be recognized in six of the ten specimens. Where preserved, it is usually better developed at the anterior end of the shell than at the posterior. The smallest specimen referable without question to *B. carinata* is 1.20 mm. long and 0.33 mm. high. This specimen shows the long hinge line, flat venter and hollow posterior spine, and differs from the larger specimens only in having slightly less well developed spines.

No articulated valves have been found, so the manner and extent of the ventral overlap is not known.

Types.—The lectotype, YPM 20392, and the figured left valve, YPM 20845, are in the collections of the Yale Peabody Museum, New Haven, Connecticut.

Genus ACANTHOSCAPHA Ulrich & Bassler, 1923

Acanthoscapha Ulrich & Bassler, 1923, p. 319; Bassler & Kellett, 1934, p. 38.
Alanella Bouček, 1936, p. 71; Henningsmoen, 1953. p. 247,265,273; Bouček & Přibyl, 1955, p. 587,615,639,640; Kesling & Sohn, 1958, p. 519–522.

Type species.—By original designation, *Beecherella navicula* Ulrich, 1891.

Diagnosis.—Smooth, elongate beecherellid ostracodes with ventro-terminal areas laterally compressed in a dorso-ventral plane; anterior and posterior ends may be produced as spines. Left valve slightly larger and overlaps right on terminodorsal and ventral borders. Duplicature better developed posteriorly.

Discussion.—The above diagnosis of the genus is essentially that given for *Alanella* Bouček by Kesling & Sohn (1958, p. 519–520). Prior to 1958, several specimens referable to *Alanella* had been picked from Beecher's collection, although none which agreed with Ulrich's description and illustrations of *Acanthoscapha* had been found. The explanation for this became apparent when the type specimens of *Acanthoscapha navicula*, which had been temporarily mislaid, were located and examined. Both specimens described by Ulrich were broken when he described the species, although he figured the more complete of these, YPM 20390, as "a perfect left valve" (Ulrich, 1891, p. 204, pl. II, fig. 8). The same figure was subsequently used to illustrate the genus by Ulrich & Bassler (1923, p. 318, fig. 2) and by Bassler & Kellett (1934, text-fig. 17, fig. 2) who reversed Ulrich's original orientation and illustrated the specimen upside down. The original of this figure, YPM 20390, and a more complete topotype specimen are shown on plate 66, figs. 16–18. As may be seen from the photographs the posterior end is broken on the type specimen which otherwise agrees with Ulrich's illustration. In view of this there seems little question that *Acanthoscapha navicula* (Ulrich) is congeneric with *Alanella bohemica* Bouček 1936, and that the genus *Acanthoscapha* Ulrich & Bassler 1923 preoccupies *Alanella* Bouček 1936.

Kesling & Sohn (1958, p. 522) referred the following species to *Alanella*. These should now be assigned to *Acanthoscapha*: *Alanella bohemica* Bouček, 1936; *A. decurtata* Bouček, 1936; *A. ? dubia* Kesling & Sohn, 1958 (new name for *Bairdia rostrata* Péneau 1929 non Issler 1908); *A. ? inermis* Kummerow, 1939; *A. lenticulata* (Stewart & Hendrix), 1945; and *A. devonica* Kesling & Sohn, 1958.

As noted in the discussion of *Beecherella*, Bassler & Kellett (1934, p. 135) transferred all the species, with the exception of the type species, originally described by Ulrich as *Beecherella*, to *Acanthoscapha*. Of these five species and one variety, only the type, *A. navicula*, belongs in the genus as redefined here.

Swartz (1936, p. 579–581) described the species *Acanthoscapha pentagonalis* from the Shriver chert in Pennsylvania. The generic assignment of this species was based on Ulrich's somewhat inaccurate diagnosis,

and, as the genus is now redefined, *A. pentagonalis* must be excluded. To judge from the holotype and paratypes, this species, like "*Beecherella*" *bloomfieldensis* Swartz & Swain, should be assigned either to *Camdenidea* Swain, 1953 or to some related genus.

ACANTHOSCAPHA NAVICULA (Ulrich) 1891
Pl. 66, figs. 16–18

Beecherella navicula Ulrich, 1891, p. 203–204, pl. II, figs. 8,9.
Acanthoscapha navicula (Ulrich). Ulrich & Bassler, 1923, p. 319, text-fig. 24, fig. 2; Bassler & Kellett, 1934, p. 38, text-fig. 17, fig. 2.

Diagnosis.—*Acanthoscapha* with long, nearly straight dorsal margin, ending in spines, posterior spine larger, hollow. Length about four times as great as height. Ventroterminal compressed areas well developed.

Description of types.—A slide in the collections of the Yale Peabody Museum contains two specimens, labeled "*Beecherella? navicula*, Types, Low. Helderberg gr. Albany Co., N. Y." These are the specimens illustrated by Ulrich (1891, pl. 2, figs. 8 and 9). These specimens, which were not numbered, are here assigned the number YPM 20390, for the original of fig. 8, and YPM 20391 for the original of fig. 9. Ulrich apparently considered both specimens as cotypes, but the most complete specimen, YPM 20390 is here designated the lectotype of the species. The lectotype is a left valve, incomplete at the posterior end, 2.10 mm. long and 0.62 mm. high (pl. 66, figs. 17,18). The dorsum is long and straight, and the anterior spine, 0.23 mm. long, turns upward from the dorsum at a low angle. Anteroventrally and posteroventrally the valve is flattened, but medioventrally the margin forms a lip overlapping the right valve. The surface is smooth, except where roughened by adventitious silica. Internally, the duplicature is present at both ends of the shell as a shelf-like thickening of the free margin. The anterior spine shows a groove or channel where it wrapped around the spine on the right valve. The hinge is obscured by the silicification, but is probably simple. No muscle scar can be determined.

Discussion.—The orientation of the type given above may be open to question, since it is difficult to orient a species as nearly equally ended as *Acanthoscapha*. In studying the topotype specimens, it was decided to consider the end with the larger spines as posterior. These spines are more nearly parallel to the hinge line, whereas the anterior spines bend upward at a slight angle. Because the one remaining spine on the lectotype also bends upward, it is assumed that it is anterior in position, and that the lectotype is a left valve. It is of interest that the orientation here given is the same as that in Ulrich's original description, although Ulrich & Bassler (1923, p. 318, text-fig. 24, fig. 2) considered the spine posterior and reversed the dorsal and ventral positions. It is also interesting that Ulrich (1891, p. 203, pl. II, figs. 8,9) both described and illustrated the duplicature as a ridge, "Running nearly parallel with the anterior edge. . . ."

The specimen illustrated by Ulrich (1891, pl. II, fig. 9) was considered by him to be the broken anterior end of a right valve, which he described as having a slightly longer and stronger spine than on the left. Reexamination of this specimen suggests that it is more likely to be the posterior end of the left valve.

Ulrich (1891, p. 204) had considered distinguishing "*Beecherella*" *navicula* as a separate genus on the basis of its internal structure (presumably the duplicature), and with the type specimens is a note on a separate piece of paper which reads as follows: "*Acanthella* n. gen. (Ulrich!) proposed for these in English edit. Zittel's Textbook of Paleontology." However, there is no record of this name being used for *A. navicula* in either the first or second English edition of Zittel's Textbook (1900, 1913), and as the first edition includes a note stating that the section on ostracodes was condensed from a manuscript provided by Mr. Ulrich, it seems probable that this name was never published. In any case, the name is preoccupied by *Acanthella* Schmidt 1862 for a sponge, and *Acanthella* Allman 1883 for a coelenterate (Neave, 1939, p. 9).

In addition to the types described by Ulrich, the topotype collection has yielded six specimens of *Acanthoscapha navicula*, two of which are complete carapaces. This additional material has been used to prepare the revised specific diagnosis. The illustrated complete carapace, YPM 20844 (pl. 66, fig. 16), is 1.84 mm. long and 0.50

mm. high. The second carapace is 2.30 mm. long and 0.69 mm. high. The height of both is between one-third and one-quarter of the length. In both of these specimens the terminal spines are broken, and, as the above measurements of length were made along the dorsum, the length including the spines would be somewhat greater. The anterior spines turn up at a slight angle to the hingeline. The anteroventral and posteroventral flattened flanges are well developed. In dorsal view the sides of the carapace are nearly parallel in the median part of the shell. The hinge line is not entrenched. Ventrally the left valve overlaps the right slightly in the median part of the shell, but in the flanged part of the free margin the valves meet in a plane, with no overlap. The anteroventral flattened flange is shorter and less well developed than the posteroventral flange. The anterior spine on the left valve seems to be somewhat better developed than that on the right.

Acanthoscapha navicula Ulrich differs from *A. bohemica* (Bouček) in being proportionately somewhat less attenuate, and having a less distinct flattened ventral flange. *Acanthoscapha decurtata* (Bouček), according to the original illustration of the holotype (Bouček, 1936, pl. V, fig. 1) differs from *A. navicula* in having the flattened flange extending along the entire venter, with no area of overlap. *Acanthoscapha devonica* (Kesling & Sohn) lacks the terminal spines of *A. navicula*, and *A. lenticulata* (Stewart & Hendrix) is not as attentuated.

Ulrich's original conception of *Acanthoscapha* as an elongate ostracode with a spine at one end and with the other end rounded may have been influenced by the occurrence in Beecher's collection of an undescribed species of the type formerly referred to *Bythocypris*. This form is similar to Ulrich's original definition of the genus in having a terminal spine on one end and being rounded on the other. It is elongate like *A. navicula*, but differs in having a curved dorsum, no flattened anteroventral and posteroventral flanges, and having a distinct anterior vestibule. This form is rare and, as not enough specimens are available to determine all of its characteristics its systematic position is uncertain.

Types.—The lectotype, YPM 20390, the lectoparatype, YPM 20391, and the figured complete carapace, YPM 20844, are in the collections of the Yale Peabody Museum, New Haven, Connecticut.

FAMILY UNCERTAIN

Genus JANUSELLA Roth 1929

Type species.—*Janusella biceratina* Roth, 1929, p. 363–365, pl. 37, figs. 23 a–c. Holotype, USNM 80665.

Diagnosis.—Asymmetrical ostracodes with a hollow, dorsally directed spine or node on the dorsum of the left valve and a latero-posteriorly directed spine on the posterior of the right valve. Left valve overlaps right ventrally, and fits into lip in right valve on anterior margin. Hinge simple. Muscle scar not known.

Discussion.—Roth gave no generic diagnosis in his description of *Janusella biceratina*, and considered the species rare, as he had only three specimens. Two additional species are now known, one of which is as yet undescribed, and the other is discussed in this paper. The above diagnosis is based on specimens of all three species. The resemblance of the right valve of *Janusella* to that of *Krausella* Ulrich, 1894 suggests that the genera may be related, as noted by Roth (1929, p. 364). As neither genus possesses a duplicature they cannot be placed in the Beecherellidae as redefined, and are listed here as "Family uncertain." At present, the stratigraphic position of only two species of *Janusella* is known and both species come from beds of Helderbergian age.

JANUSELLA SUBTUMIDA (Ulrich) 1891

Pl. 66, figs. 7–10

Beecherella subtumida Ulrich, 1891, p. 200–201, pl. 11, figs. 5–7.

Acanthoscapha subtumida (Ulrich). Bassler & Kellett, 1934, p. 145.

Diagnosis.—Left valve with well developed sharp spine and incipient node on posterior end. Right valve evenly curved in dorsal outline, anterior lip and posterior spine well developed.

Description of types.—The type material consists of four right valves, two in the collections of the Yale Peabody Museum and two in the collections of the U. S. National Museum. Ulrich (1891, p. 102) states that the type is in Dr. C. E. Beecher's collection, which would indicate that one of the speci-

mens at Yale is the holotype, although the specimens in the National Museum are labeled "holotypes" (sic.) in what appears to be Ulrich's handwriting. As, under these circumstances, it is necessary to designate a lectotype, specimen YPM 20395 is so designated, this being the most nearly complete of the four available.

The lectotype is 1.54 mm. long and 0.70 mm. high. The posterior spine, which is broken at the tip, protrudes about 0.15 mm. beyond the contact margin of the valve. The dorsal margin is curved, but the hinge line as seen on the interior of the valve is straight, and at a slight angle to the ventral margin, which is nearly straight. The anterior margin is curved, and the posterior acuminate ventrally, terminating in a spine which is nearly in a line with the ventral margin. At the anterior end of the shell there is a lip-like projection which extends beyond the contact margin in the plane of the valve. The valve is tumid at its midpoint. The muscle scar is not preserved. The shell surface is smooth.

The lectoparatype, YPM 20396, is similar to the lectotype, but is incomplete along the dorsal margin. Of the two lectoparatypes in the National Museum, both numbered USNM 41817, one is complete except for the posterior spine (pl. 66, fig. 7), the other is broken in half.

Discussion.—In addition to the type material described above, about 70 specimens of *Janusella subtumida*, all right valves, have been receovered from Beecher's collection. Ulrich (1891, p. 203), in describing *Beecherella cristata*, states that in this species the left valve is without a spine, whereas the right valve has a posterior spine, and suggests that "*B. subtumida*, known only from right valves, is evidently a related form, and it is possible that in it too the left valve is spineless, which may account for its non-recognition." From the same lot containing the right valves, about 45 left valves with the characteristic dorsal spine of *Janusella* have been recovered. The outline of the contact margins of both valves and the absence of any other left valves in the collections which could fit "*Beecherella*" *subtumida* suggest strongly that these valves belong together, and the species has accordingly been placed in *Janusella*, although as yet no articulated valves have been found. This assignment is strengthened by comparison of *Janusella subtumida* with *J. biceratina* Roth, the type of the genus. The holotype of *J. biceratina*, USNM 80665, which is crushed, and two uncrushed topotype specimens all show indications of the anterior lip on the right valve into which the edge of the left valve fits. Neither this lip, nor any other marginal structure, is present on the left valve.

The additional material of *J. subtumida* permits a more expanded description of the species than was possible to Ulrich. The smallest left valve is 0.65 mm. long and 0.46 mm. high, including the dorsal spine, the smallest right valve 0.69 mm. long, including the posterior spine, and 0.35 mm. high. The largest left valve is 1.92 mm. long and 1.38 mm. high, including the dorsal spine, the largest right valve is 1.98 mm. long, including the unbroken posterior spine, and 0.84 mm. high. There is little apparent change in outline or other features between the smallest instars and the largest, although such characteristics as length of spine and proportional length of shell appear to vary between specimens of the same general size. The smallest molts of the left valve seem to have proportionally smaller dorsal spines, and the posterior node or swelling is inconspicuous.

The most distinctive specific character of *Janusella subtumida* is the node-like posterior swelling on the left valve. This feature is lacking on *Janusella biceratina* and on an undescribed species of *Janusella* from the Gaspé Peninsula.

Types.—The lectotype, YPM 20395, and the lectoparatype YPM 20396, are in the collections of Yale University, New Haven, Connecticut. The lectoparatypes USNM 41817 are in the collections of the U. S. National Museum, Washington, D. C.

GENUS UNCERTAIN

"BEECHERELLA" ANGULARIS Ulrich 1891
Pl. 66, figs. 11–15

Beecherella angularis Ulrich, 1891, p. 204, pl. II, figs. 10–12.
Acanthoscapha angularis (Ulrich). Bassler & Kellett, 1934, p. 145.

Description of type.—The holotype, YPM 20397, is a right valve with an arcuate

dorsum, a rounded anterior margin, a flat venter terminating in a small spine, and a gently curved posterior margin which joins the ventral margin at the small spine. In end view the valve is widest through the flattened venter. The hinge is straight, simple, parallel to the ventral margin, and about one-half to one-third the total length of the valve. The muscle scar is not preserved, and the duplicature is not present. The shell surface is smooth. There is a distinct but low carina where the ventral surface joins the lateral surface at an acute angle. The cross section of the valve is triangular. It is 1.40 mm. long, 0.70 mm. high and 0.40 mm. wide.

Discussion.—Ulrich's description was based on one specimen, the holotype. Beecher's collection has now yielded 50 additional valves, of which 26 are left valves and 24 are right valves, as well as one complete carapace. The carapace is poorly preserved, but does show details of the ventral overlap and the general cross-section of the shell. A more complete description of the species can be made on the basis of this supplementary material. The carapace is nearly equivalved, with a markedly flattened venter and triangular cross-section. The left valve is slightly larger and overlaps the right ventrally. The hinge is slightly entrenched and is a modified tongue-and-groove type; apparently a ridge on the left valve fits into a groove on the right. There is no indication of a muscle scar on any of the specimens. The posterior spine can more properly be considered a hemispine, since each valve contributes half of what appears as a spine on the closed carapace. No traces of a duplicature are preserved on any of the specimens. There is apparently little change in proportions and outline from the younger instars to the older.

Ulrich (1891, p. 204) originally assigned this species to *Beecherella*, presumably because the triangular cross-section is reminiscent of *B. carinata*, although the differences were sufficient so that the label with the type reads "*Beecherella? angularis.*" It was subsequently placed in *Acanthoscapha* by Bassler & Kellett (1934, p. 145), because at that time the genus included ostracodes with a rounded anterior margin and a posterior spine. As these genera have been redefined, it cannot be included in either because of the absence of the duplicature, and probably belongs in a third, as yet undescribed, genus. Although the material now at hand is adequate for taxonomic purposes, it seems advisable not to propose a name until the type locality and horizon can be more definitely located, or until additional species are found at other horizons.

Ulrich's original description and illustration show the flattened margin as dorsal, and the spine as antero-dorsal. The orientation has been changed in the present paper because more complete specimens have permitted study of the hinge, and because the spine is considered more likely to be posterior in position.

Types.—The holotype, YPM 20397, and the figured carapace, YPM 20843, are in the collections of the Peabody Museum, Yale University, New Haven, Connecticut. Topotype specimens are also in the collection of the U. S. National Museum, Washington, D. C.

"BEECHERELLA" CRISTATA
Ulrich 1891
Pl. 66, figs. 1–4

Beecherella cristata Ulrich, 1891, p. 202–203, pl. II, figs. 16–18.
Acanthoscapha cristata (Ulrich). Bassler & Kellett, 1934, p. 145.

Description of types.—The types consist of two specimens, both labeled USNM 41816. One of these, the anterior half of a carapace (pl. 66, fig. 3), is labeled "Type," and apparently at some later date the prefix "Holo-" was written in front of the original designation. This is presumably the specimen illustrated by Ulrich (pl. II, figs. 16–18), as he shows and describes a whole carapace. The back of the label with this specimen has a note "spine broken away in 1894, E. O. U." The other specimen is a right valve in good condition except that the spine is broken above the base (pl. 66, fig. 4). There is no indication on the label that this specimen was considered a type by Ulrich, other than the fact that it carries the same number as the figured specimen. This specimen was not illustrated, but was presumably used by Ulrich in his conception of the species. Although Ulrich did not specifically

designate a holotype, there is little doubt that the carapace, now broken, which was described and illustrated is the holotype. Unfortunately, the specific characters are no longer recognizable from this specimen.

The holotype, as it now exists, consists of a part of the anterior portion of a carapace (pl. 66, fig. 3). The anterior part of the left valve overlaps the right, and projects in a small, triangular, flap-like spine. The paratype is a right valve, with the stump of a small, subcylindrical posterior spine and an anterior lip-like flange which presumably fits against the left valve. The maximum length, exclusive of the spine, is 1.39 mm., and the maximum height is 0.60 mm. The spine is about 0.08 mm. long. The shell surface is smooth. The dorsal and posterior margins are evenly curved. The peg-like posterior spine projects from the surface of the valve in front of the posterior contact margin. The anterior margin has a slightly angular break in profile at about two-thirds the height of the valve, but is otherwise evenly curved. The ventral margin is slightly sinuate. Internally the hinge appears to be simple, fairly short and straight, and located in the posterior half of the valve. The anterior lip is well developed and projects beyond the contact margin of the valve, much as in *Janusella subtumida* (Ulrich). The muscle scar is not preserved, and there are no indications of a duplicature.

Discussion.—Ulrich originally described the spine, here considered posterior, as anterior in position. The orientation here proposed is based on the currently recognized criteria applied to ostracodes.

Ulrich (1891, p. 202,203, pl. II, figs. 16,19) describes and illustrates a "crest" or ridge on the spinose right valve parallel to and slightly below the "dorsal" margin. This "crest" is no longer visible on the holotype, and is not present in the paratype right valve, where it should be, according to Ulrich's illustration. No such crest has been observed on 12 topotype specimens which are conspecific with the paratype, and also agree in all other characters with the holotype. It therefore seems probable that the crest was adventitious silica, and not a natural feature of the shell surface. This is likely in view of the preservation of other specimens in Beecher's collections, many of which have bits of silica adhering to them. The crest is therefore considered here not to be a specific character.

The topotypes which include six complete carapaces, as well as separated right and left valves, permit some additional observations about the species. The left valve, as noted by Ulrich (1891, p. 203), differs markedly from the right. Ulrich describes a "narrow flattened border at each end" of the left valve. This border is present in the topotypes, where it is produced into a small flap-like spine, so that the lateral outline of the left valve is acuminate at both ends. The left valve lacks the anterior lip present in the right valve. In lateral outline, a complete carapace appears to have a spine at each end, the anterior one projecting from the left valve, the posterior from the right. The marked asymmetry was noted by Ulrich, who stated that if the valves were not found together, they would probably be assigned to different species, if not different genera.

This species probably represents an as yet undescribed genus, possibly related to *Krausella* and *Janusella*. Since the type locality is uncertain, the stratigraphic position not well established, and the holotype broken, it is not considered advisable to describe a new genus on the basis of the material at hand. A species that may be congeneric with "*Beecherella*" *cristata* has been found in the Upper Silurian of Maine.

Types.—The holotype and paratype, both numbered USNM 41816, are in the collections of the U. S. National Museum, Washington, D. C.

"BEECHERELLA" SUBTUMIDA var. INTERMEDIA Ulrich 1891
(*nomen dubium*)
Pl. 66, fig. 5

Beecherella subtumida var. *intermedia* Ulrich, 1891, p. 201–202, pl. II, fig. 15.
Acanthoscapha subtumida intermedia (Ulrich). Bassler & Kellett, 1934, p. 145.

Description of type.—The holotype is a right valve, broken at the posterior end. The present maximum length is 0.94 mm., the maximum height is 0.54 mm. The dorsal margin is curved, the maximum height being anterior to the mid-point of the valve. The anterior margin is evenly rounded, and the

ventral margin is nearly straight. The anterior end of the shell has a small lip like those of *Janusella subtumida* and *"Beecherella" cristata*. There is no indication of a duplicature or a muscle scar. The hinge appears to be simple.

Discussion.—According to Ulrich's original description, the holotype of this species originally had a posterior spine, which is now missing. On the basis of his discussion and what remains of the type, the specimen might be either a juvenile right valve of *Janusella subtumida*, a right valve of *"Beecherella" cristata*, or a distinct species. The first mentioned alternative is the most probable. Since no specimens which can be certainly identified with Ulrich's description have been found in the topotype collections, and since the species can no longer be recognized from the holotype, the name *"Beecherella" subtumida intermedia* should be regarded as a *nomen dubium*.

Type.—The holotype, USNM 41818, is in the collections of the U. S. National Museum, Washington, D. C.

"BEECHERELLA" OVATA Ulrich 1891
(*nomen dubium*)
Pl. 66, fig. 6

Beecherella ovata Ulrich, 1891, p. 202, pl. II, figs. 13,14.
Acanthoscapha ovata (Ulrich). Bassler & Kellett, 1934, p. 145.

Description of type.—The holotype is an incomplete left(?) valve; it is, exclusive of the spine, 1.54 mm. long and 1.00 mm. high. The anterior, dorsal, and part of the ventral margins are broken; the posterior margin is relatively complete and is subelliptical in outline. The interior of the valve is filled with adventitious silica. The spine is about 0.40 mm. long and rises from the posteroventral(?) slope of the valve, above the contact margin. Anterior to it is a shallow depression, which appears to merge dorsally into a fairly deep median pit. The shell surface is grainy, and the silicification appears more crude than in other ostracodes from the same collection. This may indicate a difference in the original shell composition.

Discussion.—The preservation of the holotype is so poor that it is not possible to determine the relationships of this species, although the median pit indicates that it should not be referred to *Beecherella* as redefined. Possibly it is part of an undescribed thlipsurid, but the broken margins inhibit any precise classification. No specimens which could conceivably be conspecific have been found in the topotype material picked. Under these circumstances, the species is here considered unrecognizable and a *nomen dubium*.

Type.—The holotype, YPM 20394, is in the collections of the Yale Peabody Museum, New Haven, Connecticut.

LITERATURE CITED

BASSLER, R. S., & KELLETT, BETTY, 1934, Bibliographic index of Paleozoic Ostracoda: Geol. Soc. America Special Papers, no. 1, xiii+500 p., 24 text-figs.

BEECHER, C. E., 1893, Larval forms of trilobites from the Lower Helderberg group: Am. Jour. Sci., ser. 3, v. 46, p. 142–147, pl. 2.

BOUČEK, BEDŘICH, 1936, Die Ostracoden des böhmischen Ludlows: Neues Jahrb., Beil.-Bd. Abt. B, Band 76, Heft 1, p. 31–98, pls. 2–6, text-fig.

—— & PŘIBYL, ALOIS, 1955, On the Silurian ostracodes and the stratigraphy of the Budňany bed from the immediate vicinity of the Kosov and the Kolednik near Beroun: Czechoslovakia, Ústřed. Ústav. Geol., Sborník, v. 21, Pal. 1954, p. 577–622 (1–86), pls. 28–34 (1–7). [Russian and English summaries.]

GIBSON, L. B., 1955, Upper Devonian Ostracoda from the Cerro Gordo formation of Iowa: Bull. Am. Paleontology, v. 35, no. 154, 34 p., 2 pls.

GIRTY, G. H., 1895, A revision of the sponges and coelenterates of the lower Helderberg group of New York: Ann. Rept. State Geol., New York, for 1894, p. 261–309, 7 pls.

HENNINGSMOEN, GUNNAR, 1953, Classification of Paleozoic straight-hinged ostracods: Norsk geol. Tidsskr., v. 31, p. 185–288, pls. 1,2.

KESLING, R. V., & SOHN, I. G., 1958, The Paleozoic ostracode genus *Alanella* Bouček 1936: Jour. Paleontology, v. 33, no. 3, p. 517–524, pl. 78, text-figs.

KUMMEROW, E. H. E., 1939, Die Ostracoden und Phyllopoden des deutschen Unterkarbons: Preuss. geol. Landesanstalt, Abh., Neue Folge, Heft 194, 107 p., 7 pls.

MERTENS, ERWIN, 1958, Zur Kenntnis der Ordnung Ostracoda, (Crustacea): Geol. Jahrbuch, Band 75, p. 311–318, 11 tables.

NEAVE, S. A., 1939, Nomenclator Zoologicus, v. I, 957 p., London, Zoological Soc. London.

PŘIBYL, ALOIS, 1953, On some new ostracodes of the Lower and Middle Devonian of Bohemia: Česká Akad. věd a Umění, Bull. Internat., Prague, LII Année (1951), p. 15–51, pls. 1–5.

—— 1954, A contribution to the study of the ostracds of the Bohemian Devonian and their stratigraphical significance: Czechoslovakia, Ústřed. Ústav. Geol., Sborník, v. 21, Pal., p. 161–301, pls. 1–5.

POKORNÝ, VLADIMIR, 1950. The ostracods of the Middle Devonian Red Coral Limestones of Čelechovice: Czechoslovakia Státni Geol. Ústav., Sborník, sv. 17, p. 513–632, 5 pls.

ROTH, ROBERT, 1929, Some ostracodes from the Haragan marl, Devonian, of Oklahoma: Jour. Paleontology, v. 3, no. 4, p. 327–372, pls. 35–38.

STEWART, G. A., & HENDRIX, W. E., 1945, Ostracoda of the Olentangy shale, Franklin and Delaware Counties, Ohio: Jour. Paleontology, v. 19, no. 2, p. 96–115, pls. 11,12.

SWAIN, F. M., 1953, Devonian Ostracoda from Tennessee: Jour. Paleontology, v. 32, no. 2, p. 257–284, pls. 37–39, text-figs.

SWARTZ, F. M., 1936, Revision of the Primitiidae and Beyrichiidae, with new Ostracoda from the Lower Devonian of Pennsylvania: Jour. Paleontology, v. 10, no. 7, p. 541–586, pls. 78–89.

—— & SWAIN, F. M., 1941, Ostracodes of the Middle Devonian Onondaga beds of Central Pennsylvania: Geol. Soc. America, Bull., v. 52, p. 381–458, 8 pls., 2 figs.

TRIEBEL, ERICH, 1941, Zur Morphologie und Ökologie der fossilen Ostracoden, mit Beschreibung einiger neuer Gattungen und Arten: Senckenbergiana, v. 23,no. 416, p. 294–400, 15 pls.

ULRICH, E. O., 1891, *Beecherella*, a new genus of lower Helderberg Ostracoda: Am. Geologist, v. 8, no. 4, p. 197–205, pl. 2.

—— 1894, (1897), The lower Silurian Ostracoda of Minnesota: Minnesota Geol. and Nat. Hist. Surv., Report v. 3, pt. 2, chap. 7, p. 629–693, pls. 43–46.

—— & BASSLER, R. S., 1923, Paleozoic Ostracoda: Their morphology, classification and occurrence, *in* Maryland Geol. Survey, Silurian vol., p. 271–291, text-figs. 11–26.

WHITTINGTON, H. B., 1956a, Beecher's supposed odontopleurid protaspis is a phacopid: Jour. Paleontology, v. 30, no. 1, p. 104–109, pl. 24, text-figs. 1,2.

—— 1956b, Beecher's lichid protaspis and *Acanthopyge consanquinea*, (Trilobita): Jour. Paleontology, v. 30, no. 5, p. 1200–1204, pl. 131, 1 text-fig.

ZITTEL, K. A. VON, 1900, Textbook of paleontology, v. 1, pt. 2, C. R. Eastman ed., first English edition, Ostracoda by E. O. Ulrich, p. 642–648, figs. 1337–1354; 1913, v. 1, second English edition, Ostracoda by R. S. Bassler, p. 735–742, figs. 1423–1436.

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THE OSTRACODE FAMILY BEROUNELLIDAE, NEW[1]

I. G. SOHN AND JEAN M. BERDAN
U. S. Geological Survey, Washington, D. C.

ABSTRACT—The family Berounellidae is erected for the Paleozoic genera *Berounella* Bouček, 1936, and *Kirkbyellina* Kummerow, 1939. Specimens of undescribed species of *Berounella* are illustrated for the first time in North America.

INTRODUCTION

IN PREPARING the descriptions of genera for the forthcoming volume Q (Ostracoda) of the Treatise on Invertebrate Paleontology, Sohn was assigned the family Kirkbyidae and Berdan the family Beecherellidae. As a result of discussion between the authors, it became apparent that the genera *Kirkbyellina*, which Sohn had rejected from the *Kirkbyidae*, and *Berounella*, which Berdan had rejected from the Beecherellidae, showed remarkable resemblances and should be grouped together in a new family, Berounellidae, here proposed.

The genus *Kirkbyellina* Kummerow 1939 was described in the Kirkbyidae by the original author. Agnew (1944, p. 219) referred it to *incertae sedis*, and Mertens (1958, pl. 7) placed it in *incertae familie*. *Berounella* Bouček 1936 was assigned to the Beyrichiidae by Bouček (1936, p. 65). This assignment was questioned by Schmidt (1941, p. 24), and Agnew (1942, p. 757) placed it in ?Beecherellidae. Later Henningsmoen (1953, p. 247, 248, 273) and Mertens (1958, pl. 7) transferred it to the Alanellidae.

Specimens assigned to *Berounella* from silicified residues of limestone from New York and Nevada digested with acid have yielded additional information on the structure of the posterior projection and demonstrated the presence of a duplicature in this unusual group of ostracodes. Specimens from New York from the collections of C. E. Beecher in the Yale Peabody Museum were loaned to the authors by Prof. C. O. Dunbar and Dr. Karl M. Waagé.

Order PODOCOPIDA Sars 1865
Family BEROUNELLIDAE n. fam.

Small, subquadrate, lobed and spinose ostracodes with a posterior extension of the dorsal margin as a straight, narrow tube that, where unbroken, is equal to half or more of the greatest length of the rest of the valve. No velate structure. Hingement simple, overlap inconspicuous, surface smooth or reticulated. Duplicature present. Sil.-Dev., Miss.(?).

Discussion.—The most characteristic feature of the two genera included in this family is the extension of the dorsal margin as a long, hollow tube. In *Berounella*, this tube is common to both valves, each having a posterior projection which is semicircular in cross-section. As far as we know, nothing resembling this structure occurs in any other group of ostracodes. Many ostracodes have posterior spines, but these spines do not consist of a tubular structure shared equally by both valves. *Cytheropteron fluitans* Bonnema, 1941, from the Cretaceous of Holland, has a short posterior extension that superficially resembles this structure, but is described as having a crenulate merodont hinge.

Genus BEROUNELLA Bouček, 1936

Berounella Bouček, 1936, p. 65.

Type species.—By original designation, *Berounella rostrata* Bouček, 1936, p. 66, pl. 4, fig. 8a,b, Upper Silurian, eβ, Budňany, Czechoslovakia.

Diagnosis.—Trilobate, spinose dorso-anterior margin, with or without additional spines on the surface of the valves.

Stratigraphic range.—Upper Silurian to Middle Devonian, Europe and North America.

Discussion.—Bouček (1936, p. 66) based his description of the type and only species of this genus on three separated valves. His original diagnosis of *Berounella* is translated as follows: "Elongate Beyrichiidae with long, straight hinge margin, which is drawn out on both ends into two spine-like beaks.

[1] Publication authorized by the Director, U. S. Geological Survey.

Ventral margin is long and straight, with a 'Saum.' [Ventro-lateral pinching of the valves, see Kesling and Sohn, 1958, p. 518]. A sharply indented median sulcus and a shorter anterior sulcus divide the lateral surface of the valves into three unequal lobes."

In the description of *B. rostrata*, Bouček states further that the posterior projection extends backward as a prolongation of the hingeline and the anterior is directed obliquely upward. The holotype of *B. rostrata* has the following measurements: length 1.30 mm., height 0.40 mm., width 0.25 mm. The occurrence is given as rare in gray, ostracode rich platy limestone at the passage between eβ and eγ near Budňany (Javorka).

Twenty-nine separate valves and four carapaces of a species considered by us congeneric with *Berounella rostrata* Bouček have been picked from silicified residues of Kalkberg limestone (Lower Devonian), New York. The limestone was collected and etched by C. E. Beecher in the late nineteenth century. One specimen of another species of *Berounella* has been found in silicified residues of an unnamed Middle Devonian (?) formation from the Cortez Range, Eureka County, Nevada (pl. 67, figs. 5,6). Neither species is to be described at the present time, because of inadequately preserved specimens and uncertain locality data. However, this additional material provides further information concerning the genus, and is therefore illustrated.

As may be seen from plate 67, figures 7–15, the silicified specimens from the Kalkberg limestone show a distinct duplicature. It is therefore necessary to remove the genus from the family Beyrichiidae (Paleocopida), where it was placed by Bouček, and to place it in a new family in the order Podocopida. The anterior spine appears to be solid, and in the specimens from the Kalkberg limestone is better developed on the right valve than on the left. Bouček (1936, Pl. IV, fig. 8a) illustrates a left valve on which the spine is restored, suggesting that this might also be true of the type species. Many specimens from the Kalkberg limestone show a development of small finger-like spines along the dorsoanterior margin, especially on the left valves. These spines, as well as spines projecting posteroventrally or laterally from the posterior part of the valve are believed to be of specific significance. The posterior "spine" is an extension of each valve along the hingeline, forming a long, hollow tube which in one of the most complete examples is slightly greater than the greatest length of the carapace excluding the posterior projection (pl. 67, fig. 11).

The specimens available to us are too crudely silicified to provide any information on surface ornamentation, nor does Bouček mention the details of the surface in his original description.

The valves are nearly symmetrical, the left valve slightly overlapping the right on the ventral margin. The flattened contact margin mentioned by Bouček is developed only on the anteroventral and part of the posteroventral margins of our material.

Genus KIRKBYELLINA Kummerow 1939

Kirkbyellina Kummerow, 1939, p. 30.

Type species.—By original designation, *Kirkbyellina styliolata* Kummerow, 1939, p. 31, pl. 3, figs. 5a,5b, Middle Viséan, Binsfeldhammer bei Stolberg, Rheinland.

Diagnosis.—Small, long ostracodes with a wide subcentral sulcus surrounded by a wide U-shaped lobe that has a knob in the dorsoanterior portion of the shell and trends toward the dorsoposterior projection.

Stratigraphic range.—Lower Carboniferous (?), Europe.

Discussion.—Kummerow (1939, p. 30) gave the following diagnosis for *Kirkbyellina*, which is translated as follows:

"Small, longish shells with a strong horizontal process." His description of *K. styliolata*, the type and only species, is as follows (Kummerow, 1939, p. 31):

"Shell small, elongated. Dorsal margin long, straight, with a strong horizontal process on the anterior end that is incompletely preserved, and perhaps exceeds the length of the shell. Anterior and posterior margins rounded. Ventral margin shallowly convex, almost straight. A deep sulcus is located behind the mid point of the dorsal margin and reaches almost to the middle of the valve. Behind it lies a prominent hemispherical knob. From its lower side a lobe curves under the sulcus toward the anterior

and terminates about ⅓ of the length of the valve. It slopes steeply toward the ventral, and gradually toward the dorsal margin.

The flattened contact margin is broad along the anterior part of the ventral margin and narrow along the posterior part. The point of greatest height is the anterior. The upper surface appears to be reticulated.

Measurements (*holotype*).—Length without spine 0.73 mm., height 0.37 mm., width 0.26 mm.

Occurrence.—Binsfeldhammer bei Stolberg, Rheinland: Middle Viséan, S".

So far as can be determined, Kummerow based *Kirkbyellina* on a single valve, which he oriented with the long process as anterior. The remarkable resemblance of *Kirkbyellina* as illustrated and described to *Berounella* suggests that both genera should have a similar orientation. The orientation of *Berounella* with the process as posterior agrees with current criteria of ostracode orientation, and the orientation of *Kirkbyellina* is therefore reversed 180°.

We have had no specimens of *Kirkbyellina* for study, and all comparisons are therefore based on Kummerow's description and illustrations. The principal difference between the two genera (pl. 67, figs. 3,4) appears to be that *Berounella* is distinctly bisulcate, but *Kirkbyellina* has only one large median sulcus.

Superficially *Kirkbyellina* resembles *Hanaites* Pokorný, 1950 and related genera because of the large subcentral sulcus, but *Hanaites* has solid short posterior spines.

The type locality of the holotype of *Kirkbyellina* is in an area of complex geologic structure. The geologic map of the region shows at Binsfeldhammer many small fault blocks of Paleozoic rocks. The possibility that the specimen was collected from older rocks cannot be overlooked. This hypothesis is supported by the lack of record of berounellid ostracodes from the Carboniferous of Europe and North America. Additional work at the type locality is necessary to verify the age of this genus.

REFERENCES

AGNEW, A. F., 1942, Bibliographic index of new genera and families of Paleozoic Ostracoda since 1934: Jour. Paleontology, v. 16, p. 756–763.

——, 1944, Addenda and errata to bibliography of Paleozoic ostracodes: Jour. Paleontology, v. 18, p. 218–219.

BONNEMA, J. H., 1941, Ostracoden aus der Kreide des Untergrundes der nordöstlichen Niederlande: Natuurh. Maandbl., Jaarg. 30, no. 3, p. 26–29, pl. 6.

BOUČEK, BEDŘICH, 1936, Die ostracoden des böhmischen Ludlows (Stufe eβ): Neues Jahrb., Beil.-Bd. Abt. B, Band 76, Heft 1, p. 31–98, pls. 2–6, textfigs.

HENNINGSMOEN, GUNNAR, 1953, Classification of Paleozoic straight-hinged ostracods: Norsk Geol. Tidsskr., v. 31, p. 185–288.

KESLING, R. V., and SOHN, I. G., 1958, The Paleozoic ostracode *Alanella* Bouček, 1936: Jour. Paleontology, v. 32, p. 517–524, pl. 78.

KUMMEROW, E. H. E., 1939, Die Ostracoden und Phyllopoden des deutschen Unterkarbons: Preuss. Geol. Landesanstalt, Abh., neue folge, Heft 194, p. 6–107, 6 pls.

MERTENS, ERWIN, 1958, Zur Kenntnis der Ordnung *Ostracoda* (*Crustacea*): Geol. Jahrb., v. 75, p. 311–318, 11 tables.

POKORNÝ, VLADIMÍR, 1950, The ostracods of the Middle Devonian Red Coral limestone of Čelechovice: Czechoslovakia Stát. Geol. Ústav. Sbor., v. 17, Pal., p. 513–632, 5 pls.

SCHMIDT, E. A., 1941, Studien im böhmischen Caradoc (Zahořan-Stufe). 1. Ostrakoden aus den Bohdalec-schichten und über die Taxonomie der Beyrichiacea: Senck. Naturf. Ges., Abh. 454, 96 p., 5 pls.

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(*Explanation of* PLATE 67 *on next page*)

EXPLANATION OF PLATE 67

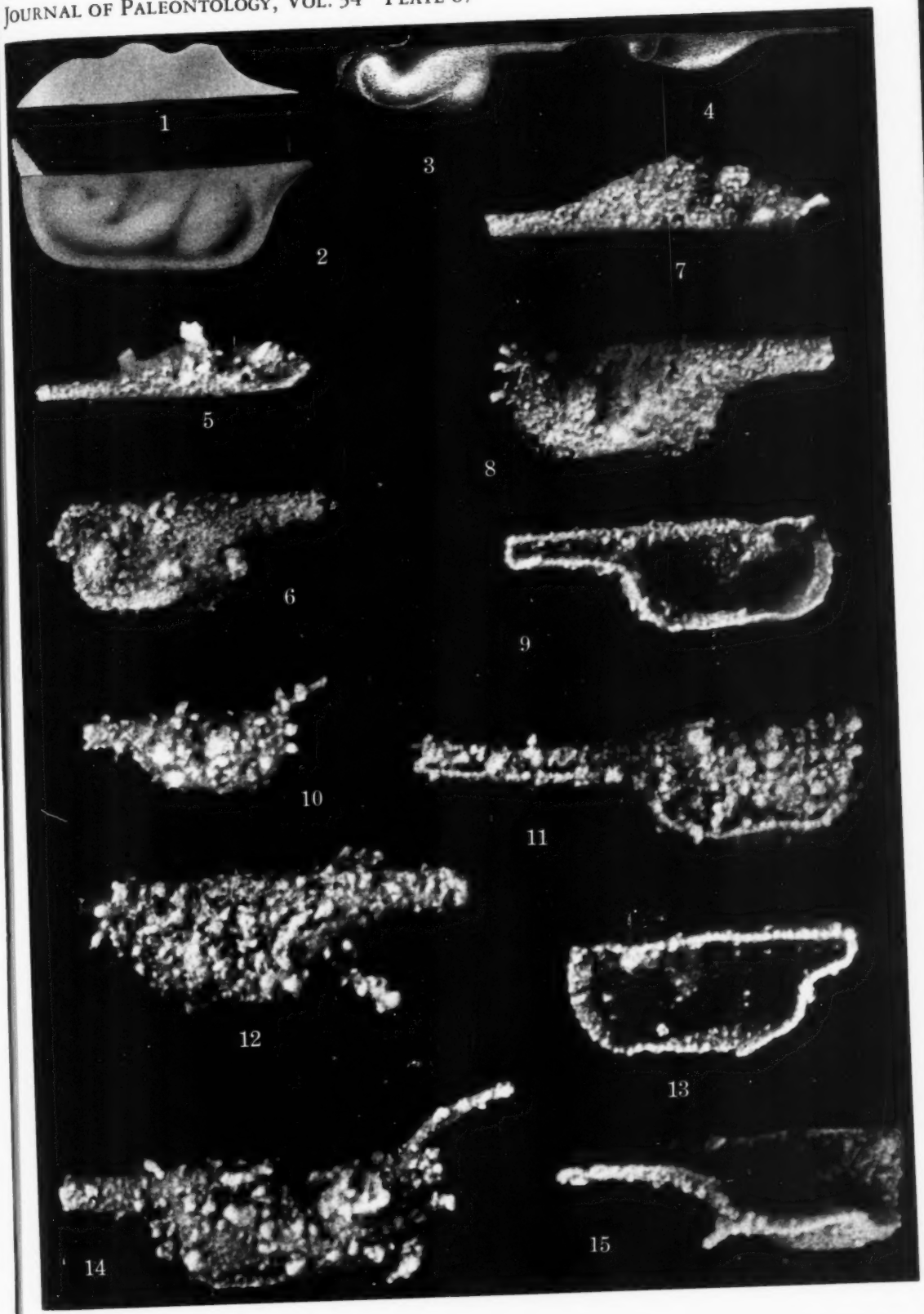
(Except where noted, magnification ×60)

FIGS. *1,2*—*Berounella rostrata* Bouček 1936, holotype, left valve, and lateral and ventral views, ×40, Upper Silurian, Bohemia. (From Bouček, 1936, Pl. IV, figs. 8a,8b).

3,4—*Kirkbyellina styliolata* Kummerow 1939, holotype, left valve, lateral and dorsal views, ×30. The thread-like line on the anterior part of fig. *3* is considered by us as not part of the specimen. Middle Viséan, Germany. (From Kummerow, 1939, Plate III, figs. 5a, 5b).

5,6—*Berounella?* sp., left valve, anterior broken, dorsal and lateral views. Middle Devonian (*?*), Cortez Range, Nevada, USGS loc. 4933-SD, figured specimen USNM no. 143012.

7–15—*Berounella* sp., *7–9*, left valve, lateral, dorsal and interior views, figured specimen YPM no. 20846, *10*, right valve of a young instar, lateral view, figured specimen YPM no. 20847, *11*, right view of carapace, slightly tilted, to show overlap, figured specimen, YPM no. 20848, *12*, left valve, lateral view, figured specimen, YPM no. 20849, *13*, interior view, figured specimen, YPM no. 20850, *14*, right valve, lateral view, figured specimen, YPM no. 20851, *15*, left valve, interior view, anterior portion missing, figured specimen, YPM no. 20852. Kalkberg limestone, Albany County, New York. YPM means Yale Peabody Museum.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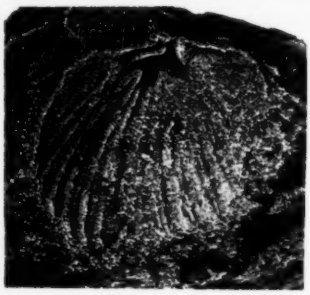

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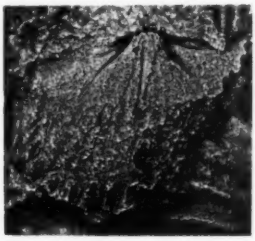

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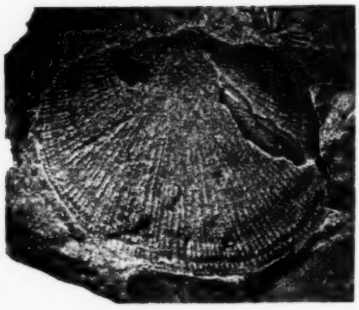

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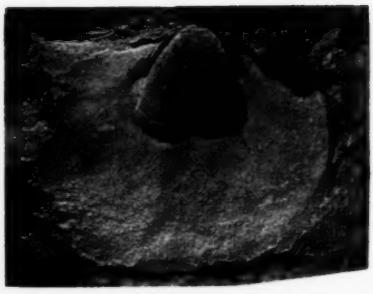

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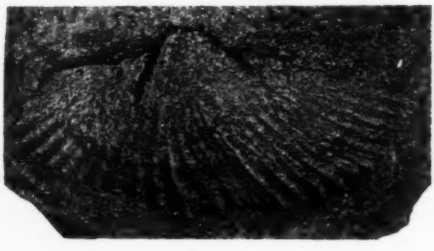

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JOURNAL OF PALEONTOLOGY, V. 34, NO. 3, P. 483–485, PL. 68, MAY, 1960

A NEW LOWER DEVONIAN STROPHEODONTID BRACHIOPOD

ARTHUR J. BOUCOT[1]

ABSTRACT—Lower Devonian brachiopods from Nova Scotia show affinities with the Rhenish faunal province. *Rhenostrophia*, a new subgenus of *Stropheodonta* is described.

INTRODUCTION

COLLECTIONS of Lower Devonian brachiopods from the Nictaux-Torbrook and Bear River areas of the Annapolis Valley, Nova Scotia, have recently been submitted to the author by Professor Charles Hickox, Colby College, Mr. George DeVries Klein, Yale University, and Mr. William Smitheringale, Geological Survey of Canada. These faunas have turned out to be of considerable interest inasmuch as they show affinities with the Rhenish faunal province, rather than with the Appalachian, and are the only Lower Devonian faunas of Rhenish affinities known in North America. A paper discussing the zoogeographic implications of these faunas, as well as their age and composition, is now being prepared for presentation at the International Geological Congress in Copenhagen. The Rhenish elements in these faunas, among which is the new subgenus *Stropheodonta* (*Rhenostrophia*) are illustrated in plate 68.

[1] Department of Geology and Geophysics, Massachusetts Institute of Technology.

SYSTEMATIC DESCRIPTION

Phylum BRACHIOPODA
Class ARTICULATA
Superfamily STROPHOMENACEA
Family STROPHEODONTIDAE
Genus STROPHEODONTA Hall, 1852, emended Williams, 1953
Subgenus RHENOSTROPHIA, new subgenus

Type species.—*Orthis subarachnoidea* D'Archiac et De Verneuil, 1842, Trans. Geol. Soc. London, 2d ser., v. 6. p. 372, pl. 36, fig. 3.

Diagnosis.—*S.* (*Rhenostrophia*) is characterized by the geniculate form of the valves.

Comparison.—*S.* (*Stropheodonta*) is non-geniculate and possesses parvicostellae which are thrown into secondary plications or costellae. *S.* (*Brachyprion*) is non-geniculate and has weakly defined muscle impressions as compared with *S.* (*Rhenostrophia*). *S.* (*Eostropheodonta*) has short dental lamellae and hinge teeth in the pedicle valve, both lacking in *S.* (*Rhenostrophia*), and is non-geniculate. The characteristic stropheo-

EXPLANATION OF PLATE 68

FIGS. *1–3*—*Tropidoleptus* sp., Bear River, Nova Scotia. *1*, impression of interior of brachial valve (×2), showing crenulated dental sockets. Geological Survey of Canada No. 14760; *2*, impression of exterior of brachial valve (×2). Geological Survey of Canada No. 14760; *3*, impression of interior of pedicle valve (×2). Geological Survey of Canada No. 14760.

4–6—*Proschizophoria* sp., Fales River, near Torbrook, Nova Scotia. *4*, impression of exterior of pedicle valve (×1). Geological Survey of Canada No. 14761a; *5*, impression of interior of brachial valve (×2). Geological Survey of Canada No. 14762; *6*, Impression of interior of pedicle valve (×1). Geological Survey of Canada No. 14761b.

7–8—*Meganteris* sp., Bear River, Nova Scotia. *7*, impression of interior of brachial valve (×1). Geological Survey of Canada No. 14763; *8*, impression of interor of brachial valve (×1), showing crenulated adductor field. Geological Survey of Canada No. 14763.

9—*Stropheodonta* (*Rhenostrophia*) sp., Bear River, Nova Scotia. Impression of interior of brachial valve (×1). Geological Survey of Canada No. 14764.

10—"*Spirifer*" cf. "*S.*" *bischofi*, Bear River, Nova Scotia. Impression of interior of pedicle valve (×1½). Geological Survey of Canada No. 14765.

dontid muscle pattern present in both valves of *S.* (*Rhenostrophia*) serves to remove it from close affinity with other groups of the Stropheodontidae such as the leptostrophids.

Exterior.—The outline of the valves varies from subcircular to laterally or longitudinally elongate but never departs far from subcircular. The brachial valve is gently concave for about two-thirds of its length and strongly geniculate for the remainder. The pedicle valve is gently convex for about two-thirds of its length and strongly geniculate for the remainder. The maximum width of both valves is at the straight hinge line. Mucronate ears are present in well preserved specimens but are usually broken off. The fine ornamentation consists of radial parvicostellae crossed by fine, irregularly spaced concentric growth lines. The interarea of the pedicle valve is gently apsacline and three to four times as long as the steeply anacline interarea of the brachial valve. The delthyrium is closed by a triangular pseudodeltidium which bears a low median fold. The geniculate portions of both valves are irregularly folded radially into loose, gently curved folds. The notothyrium is closed by a medially folded chilidium. The interareas of both valves are longitudinally grooved by the traces of the denticulations.

Interior of brachial valve.—The cardinalia consist of discrete cardinal process lobes laterally bounded by large socket plates. The posterior face of each cardinal process lobe is posteriorly inclined at about 45 degrees to the plane of the commissure. The hinge line is denticulate in large specimens for about three-quarters of its length. The muscle field, strongly impressed and longitudinally elongate in outline, is about one-half to two-thirds as long as the valve and about one-fifth as wide. The anterior half of the muscle field is bisected by a low septum. The muscle impressions consist of an elliptical, longitudinally elongate pair of foliaceous posterior adductors and a slightly smaller pair of longitudinally elongate anterior adductors separated by a septum. Both pairs of muscle impressions are laterally bounded by a high, massive muscle-bounding ridge of secondary material. The periphery of the valve bears the impress of the parvicostellae, but the remainder of the interior is coated by a layer of secondary material which thickens rapidly in a medio-posterior direction. The region immediately lateral to the muscle field is deeply pitted.

Interior of pedicle valve.—A well-developed ventral process is laterally bounded by deeply excavated process pits. Anterolaterally diverging from the process pits are muscle-bounding ridges which extend almost to the midlength before turning medially to bound the deeply impressed muscle field anteriorly. The muscle field is subcircular to longitudinally elongate in outline. The muscle-bounding ridges include an angle of almost 90 degrees. The muscle field is flabellate and consists of a pair of foliaceous, longitudinally elongate, posteriorly situated adductor impressions flanked laterally and bounded anteriorly by fasciculate diductor impressions. Both the adductor and diductor impressions are medially bisected by narrow grooves, that of the diductors corresponding in position to the septum which bisects the anterior adductors of the brachial valve. The periphery of the valve is impressed by the parvicostellae, but the remainder of the valve has a thick layer of secondary material. The portions of the valve immediately lateral of the muscle-bounding ridges are deeply pitted. The hinge line bears crenulations similar to those of the brachial valve.

Remarks.—This shell has frequently been assigned to *Leptostrophia*, probably because of the flabellate diductors in the pedicle valve and the parvicostellate non-costate ornamentation. The presence of foliaceous adductor impressions in both valves precludes this assignment (*see* Williams, 1953, for a discussion of the criteria used in the classification of the Stropheodontidae).

Types.—A holotype has never been designated for the type species. The present author is unfamiliar with the location and condition of the original specimens used by D'Archiac and De Verneuil and feels that a European paleontologist familiar with the condition of the type collections should designate the holotype.

Distribution.—In North America the subgenus is known only from the Nictaux-Torbrook and Bear River areas, Annapolis Valley, Nova Scotia. In northern Europe it is known from strata of upper Gedinnian to Emsian age in Belgium, France, England,

and Germany (Asselbergs, 1946, p. 328, *S. gigas*, middle Siegenian to upper Emsian; Drevermann, 1902, p. 114–115, pl. 14, figs. 15–17; Drevermann, 1904, p. 273–277, pl. 32, figs. 1–6). In Morocco it is known from strata of Emsian age (Termier, 1936, p. 1128, pl. 2, figs. 6–7). The subgenus may also occur in the region of the Bosphorus in strata of Emsian age (Paeckelmann and Sieverts, 1932, p. 37).

SPECIES ASSIGNED

Orthis subarachnoidea D'Archiac et De Verneuil, 1842, *op. cit.*

Leptaena (*Strophomena*) *gigas* McCoy, 1852, p. 387, pl. 2A, fig. 7.

Stropheodonta herculea Drevermann, 1904, p. 276–277.

REFERENCES CITED

Asselberghs, E., 1946, L'Éodevonien de l'Ardenne et des regions voisines: Mém. Inst. Geol. Univ. Louvain, tome 14, 598 p.

Drevermann, Fr., 1902, Die Fauna der Untercoblenzschichten von Oberstadtfeld bei Daun in der Eifel: Palaeontographica, Lief. 2, p. 73–120, pl. 4–14.

——, 1904, Die Fauna der Siegener Schichten von Seifen unweit Dierdorf (Westerwald): Palaeontographica, Bd. 50, Lief. 6, p. 229–288, pl. 28–32.

McCoy, Frederick, 1852, British Paleozoic fossils: Cambridge, University Press.

Paeckelmann, W., & Sieverts, H., 1932, Obersilurische und devonische faunen der Prinzeninseln, Bithyniens und Thraziens: Preuss. Geol. Land., Abh, N. F., Heft 142, 79 p.

Termier, H., 1936, Études géologiques sur le Maroc Central et le moyen Atlas Septentrionel: Serv. des Mines et de la Carte, tome 3, 1577 p.

Williams, Alwyn, 1953, North American and European stropheodontids: their morphology and systematics: Geol. Soc. America, Mem. 56, 67 p.

Manuscript received August 13, 1959

JOURNAL OF PALEONTOLOGY, V. 34, NO. 3, P. 486–492, PL. 69, 1 TEXT-FIG., MAY, 1960

A NEW SPECIES OF SMILODON FROM A LATE PLEISTOCENE ALLUVIAL TERRACE DEPOSIT OF THE TRINITY RIVER

BOB H. SLAUGHTER

ABSTRACT—A new species of *Smilodon*, *S. trinitiensis* is described from the Pleistocene deposits forming an alluvial terrace above the Trinity River at Dallas, Texas.

INTRODUCTION

THE second of a series of alluvial terraces rising above the Trinity River at Dallas, Texas, is the source of much of the sand and gravel used in the rapid growth of the city. During these mammoth excavations many fossils of late Pleistocene animals are uncovered. Although fossils are dug up daily, not one out of a thousand is recovered. No doubt hundreds of fossil elephants have been destroyed since the first one was recorded in 1887. The present writer has counted fifteen semi-articulated skeletons of *Mammuthus columbi* in a single pit. Until about six years ago the only collection of any consequence was that of the late Ellis W. Shuler of Southern Methodist University, Dallas. In "Fauna of the Dallas Sand Pits" R. S. Lull described one of the crania collected by Shuler as *Smilodon cf. fatalis* (Leidy). The recent discoveries of a right mandible and a left superior canine referable to *Smilodon*, prompted a re-examination of the previous find.

Both the mandible and the cranium in Shuler's collection are specifically different from all comparable material. Consequently, a new species is proposed with mandible No. 3.04 1s D.P.S.C., D.M.N.H.,* as the holotype and the cranium previously-described as *S. cf. fatalis* as the paratype.

GEOLOGY OF THE SECOND TERRACE

The second terrace (T-2) stands some 70 feet above present stream grade. Bedrock is Austin Chalk of late Cretaceous age. Alluvial deposits average about twenty feet in thickness and commonly exhibit four recognized sub-divisions. These from base to top are as follows:

Hill gravel—basal gravel five to twelve feet thick and primarily made up of limestone pebbles derived from the Washita group and redeposited marine fossils from several Cretaceous formations. Fossil bones from deep in the Hill gravel are water worn and usually fragmentary. Fossils near the top, however, probably have not been transported any great distance by the stream and are in better condition.

Lower Shuler sand—0 to 15 feet of laminated sand covering the Hill gravels. Near the base thin lenses of pebbles characterize a rejuvenation of the gravel carrying properties of the river. Fossil wood and bone are found throughout the lower Shuler sand, but the pebble lenses are the most fossiliferous. Near the top, clay bands indicate the coming of Upper Shuler conditions.

Upper Shuler clay—three to fifteen feet of sandy clay becoming less sandy near the top. The clay contains caliche nodules varying in size at different levels. Fossil locales are rare and the fossils themselves usually are in poor condition. Where fossils are found, however, they are abundant.

Richards grey-black gumbo—six to eight feet thick. The Richards can only be distinguished from the upland black soils by the presence of very small caliche nodules. No fossils have been recovered to date.

ASSOCIATED FAUNA AND ITS IMPLICATIONS

Primarily the same fauna extends throughout the terrace except for the Richards, which is essentially non-fossiliferous. Almost all late Pleistocene types are represented: *Mammut*, *Mammuthus*, *Camelops*, ground sloths, horses, and big-horned *Bison*.

* D.P.S.C.—Dallas Prehistorical Society.
D.M.N.H.—Dallas Museum of Natural History.

The fauna as well as certain geological features (presence of caliche) indicates that arid conditions were prevalent at the time of deposition. The prairie dog, jack-rabbit, and the turtle *Gopherus* may be indicative of such conditions. This climatic condition may have a bearing on the smaller size of the Dallas type of *Smilodon*, reminiscent of the smaller size of desert dwellers compared to the mountain and woodland dwellers (big-horn sheep, deer, etc.). The most common horse in the terrace is *Asinus conversidens* (Owen). J. H. Quinn (1957) gives the range of this species as "Sangamon interglacial? to late Wisconsin." C. W. Hibbard has mentioned that he knows of no *Testudo* material younger than Sangamon, and this genus is abundant throughout the T-2 terrace. Consequently, it is the opinion of the writer that the entire terrace is Sangamon though there may be some secondary filling of Peorian age. Two carbon dates made by by Humble Oil and Refining Company indicated an age in excess of 37,000 years for the upper portion of the terrace (Crook and Harris, 1957, p. 68).

The fact that only three specimens of *Smilodon* have been recovered at Dallas among hundreds of its contemporaries might lead the observor to believe that it was a truly rare beast in the area. Actually, carnivores as a whole are rare, and the *Smilodon* material represents almost half of large types collected. One specimen each of *Arctodus* sp., *Aenocyon* sp., *Ursus* sp., and coyote complete the list.

Order CARNIVORA
family FELIDAE
SMILODON TRINITIENSIS, Slaughter, new species
Pl. 69, figs. 1,3,4,7

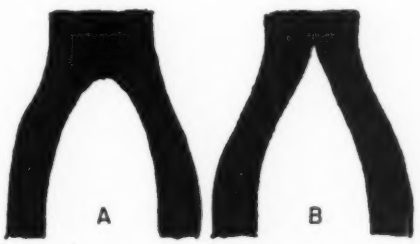
Holotype—A right mandible complete except for condylar process and incisors. No. 3.04 1s D.P.S.C. Dallas Museum of Natural History. Collected from a pebble lens near the bottom of the lower Shuler exposed by the Pemberton Hill Sand and Gravel operation at the southern city limit of Dallas.

First paratype—A cranium with complete occiput and partially complete mastoid processes. No. 1.52 up-h, Southern Methodist University. Collected from the uppermost Hill gravel in the Lagow Sand Pit four miles upstream from Pemberton Hill.

Reffered—Distal 100 mm. of left superior canine. No. 4.01 1s-h, D.P.S C. Dallas Museum of Natural History. Collected from a pebble lens near the bottom of the lower Shuler at the Roy Moore pit 600 yards downstream from Pemberton Hill.

Description of mandible, No. 3.04 1s D.P.S.C., D.M.N.H.

The mandible is more slender than that of the other species of *Smilodon* and the modern *Panthera leo*. The symphysis is strong, joining abruptly, thus changing the angle of the symphyseal considerably from that of true cats (text-fig. 1). The diastema is short and has a marked upward curvature (pl. 69, fig. 1). Bovard mentions this feature in his "Notes on Quaternary Felidae from California" as being present in some specimens of *S. californicus*. He credited it to sexual difference. The curvature in the Dallas specimen, however, is more pronounced than in any of the illustrated mandibles described by Merriam and Stock in "The Felidae of Rancho La Brea." The mental foramen occupies a spot a little posterior of that in adult specimens of other species of *Smilodon*. The canine is incisiform. $P\frac{4}{4}$ and $M\frac{1}{1}$ complete the inferior dentition. Both are strongly inclined posteriorly. $P\frac{4}{4}$ has a well developed anterior basal cusp, principal cusp or protocone (which includes a little less than half of the entire tooth's length), metacone and a posterior heel cusp. Anterior root is longer than the posterior.



TEXT-FIG. 1—a. Angle of symphyseal, *Smilodon trinitiensis* new species. b. Angle of symphyseal of true cats.

M1 is only slightly larger than P4. The metaconid blade is more than one and one-half times the length of the posterior paraconid blade and is parallel to the cingulum. Both anterior and heel cusps are present, roots more robust than all other species in the genus. It is evident that this tooth was self-sharpened by abrading against P4.

Description of cranium, No. 1.52 up-h, S.M.U.*

The writer is indebted to Robert Perkins, formerly of the S.M.U. Geology Department, for the loan of this specimen.

The brain case is larger, relative to the occiput, and more convex transversely than *S. californicus*. The sagittal crest is thin and sharp. The lamboidal crests are distinct from the sagittal to the mastoid but the lamboidal eves overhang the occiput less than in the other known types. The mastoid process is inclined forward until it touches and partially fuses with the post-glenoid process. The narrow occiput is divided by a prominent occipital ridge and is considerably trenched and embossed.

Description of left superior canine, No. 4.01 1s D.P.S.C., D.M.N.H.

The total length of the left superior canine, which is incomplete, cannot be accurately determined. The pulp cavity extends ten millimeters into the remainder as preserved. Merriam and Stock (1932, p. 46) state that the root includes about two-thirds of the tooth's total length in *S. californicus*. The estimate of the original length of the Dallas specimen on this basis is 200 mm. The tooth is compressed laterally with the outer face more convex than the inner face. There appears to be no noticeable difference in the size, curvature, or cross-section to distinguish the new type from *S. californicus* or *S. troglodytes*.

Comparison with *S. californicus*, Bovard

Comparison was made with a cast of a complete skull of *S. californicus* through the courtesy of W. W. Newcomb, Jr., director of the Texas Memorial Museum.

The Dallas mandible is smaller and more slender, relative to the cheek teeth, than *S. californicus*. The diastema is shorter and shows a more marked upward curvature. Mental foramen occupies a spot posterior of that in adult specimens of *S. californicus*. The canine is thinner transversely while P4 and M1 are considerably larger than the same teeth in like-sized mandibles of *S. californicus*. As a matter of fact, though all mandibular measurements of the Dallas specimen fall into the lower 20% of twenty-five individuals of *S. californicus* described by Merriam and Stock (1932), not a single P4 from California attains the anterior-posterior diameter of the Dallas P4, and only two inferior carnassials (M1) of the Californian type are as long anterior-posteriorly as the same tooth in the Dallas specimen. It should also be pointed out that the mandibles of *S. californicus* which contain teeth approaching the size of those in the Dallas mandible, have the largest mandibular measurements whereas the same measurements in the new species are closer to those of the smallest mandibles of *S. californicus*. When Lull described the Dallas cranium (1921) he stated:

> "The Dallas specimen differs from *S. californicus* not only in its lesser size, but in its relatively narrower occiput, the proportions of which compare more nearly with those of the tiger. The brain-case, on the other hand, is relatively larger in the Texas specimen, and the sagittal crest thinner; another distinction lies in a sharp thin verticle keel on the basi-occipital in *S. californicus*."

More complete material of *S. californicus* recovered later indicates that the basi-occipital is subject to a good deal of variation. The lamboidal eves do not overhang the occiput nearly as far in the Dallas specimen as in *S. californicus*. The occiput in the new species (pl. 69, fig. 4) is more triangular than that of the California type (pl. 69, fig. 6). The postero-lateral area of the matoid is very smooth in the Dallas specimen whereas it is a roughened surface in *S. californicus*.

Comparison with *Smilodon troglodytes* (Brown)

Brown described two species of this genus from the Conard fissure in Arkansas, *S. troglodytes* and *S. conardi*. However, after the extensive collection of *Smilodon cali-*

* S.M.U.—Southern Methodist University.

TABLE 1—MANDIBULAR AND DENTITION MEASUREMENTS

	S. californicus, Bovard. Average of 22 to 25 specimens after Merriam and Stock (1932)	*S. trinitiensis*, Slaughter, n. sp.
1. Length of symphysis along anterior border.	65.7 mm.	61.5 mm. within lower 20% of *S. californicus*
2. Least depth of ramus at diastema.	33.9 mm.	32.5 mm. within lower 20% of *S. californicus*
3. Depth of ramus below posterior border of M1.	40.3 mm.	38.5 mm. within lower 20% of *S. californicus*
4. Thickness of ramus below M1.	22.4 mm.	20 mm. within lower 20% of *S. californicus*
5. Greatest width across symphysis at flange.	53.2 mm.	42.5 mm.* only one in 25 specimens of *S. californicus* is as narrow
6. Greatest width across symphysis to outer walls of *C. alveoli*.	56.8 mm.	54 mm.* within lower 20% of *S. californicus*
7. Length from posterior edge of $\overline{C}$ to anterior edge of $P\overline{4}$.	60.1 mm.	53 mm. within lower 20% of *S. californicus*
8. Anterior-posterior diameter of $P\overline{4}$.	24.6 mm.	28 mm. larger than all 25 specimens of *S. californicus*
9. Anterior-posterior diameter of $M\overline{1}$.	28.4 mm.	30.2 mm. only 2 of 25 specimens of *S. californicus* are as large
10. Anterior-posterior diameter of protoconid blade of $M\overline{1}$.	13.4 mm.	17.4 mm.
11. Anterior-posterior diameter of $\overline{C}$.	14.8 mm.	14.4 mm.
12. Transverse diameter of $\overline{C}$.	11.5 mm.	9.8 mm. only 2 of 22 specimens of *S. californicus* are as small

* As only the right mandible was collected the measurement was doubled.

fornicus from Rancho La Brea were studied, Merriam and Stock (1932) concluded that as there was considerable variation in the sabre-tooth cats, only one of Brown's species be recognized, *S. troglodytes*, and the specimens referred to as *S. conardi* be referred to the former.

The lack of P3 in the Dallas mandible separates it from the Arkansas type. The sectorial teeth are larger in the Dallas species, but as *S. troglodytes* is represented by teeth only, it cannot be determined how the size compares relative to the mandible. The reduction of teeth being a more advanced trait, it may be suggested that the new species is slightly later geologically.

Comparison with *Smilodon nebrascensis*, Matthew

Matthew used the shorter diastema to separate this species from *S. californicus*. This is a point of agreement with *S. trinitiensis* n. sp. In bringing up this point, Matthew (1918, p. 229) states:

> "The post canine diastema is decidedly shorter than *S. californicus* jaws with which I have compared it, the cheek teeth are about the same size."

This it would seem, could affiliate the Dallas specimen to Matthew's species, but he went on to say, "canine and incisors more robust" (than in *S. californicus*). The in-

ferior canine in the new species is smaller, relative to the cheek teeth, when compared to *S. californicus*. Consequently, there would be an even more marked size difference if the canine of *S. nebrascensis* were compared to the Dallas specimen. Unfortunately, Matthew's type was not illustrated.

Comparison with *Smilodon* (*Trucifelis*) *fatalis*, (Leidy)

Leidy's type was merely a single P$\frac{4}{}$ with a small portion of the maxillary attached. In re-evaluating the species Merriam and Stock (1932, p. 8) state:

> "The tooth present represents P$\frac{4}{}$. The corresponding tooth in the smallest skull of *S. californicus* from Rancho La Brea is considerably more worn than the type of *S. fatalis*. While there is close agreement between the two specimens in width across protocone, length of paracone, and length of base of parastyle, the tooth as a whole is distinctly smaller and more slender in *S. fatalis* than in *S. californicus*. It is a noteworthy fact that the fourth upper premolar, observed in skulls of *S. californicus* from Rancho La Brea, is consistently larger than the comparable tooth of the Texas species. As a matter of fact, it is questionable whether there are any upper fourth premolars of sabre-tooth in the large collection from California asphalt deposits which approach closely the size or at least the anterior-posterior diameter of the type of *S. fatalis*."

As the superior fourth premolar is the working partner of both P$\frac{4}{}$ and M$\frac{1}{}$ in all cats, it is always larger anterior-posteriorly than either one of the inferior sectorials. So it is not unreasonable to assume that the lower sectorials (P$\frac{4}{}$ and M$\frac{1}{}$) of *S. fatalis* would be smaller than *S. californicus* as the specific difference is the smallness of the superior carnassial in the former. The main difference between *S. californicus* and *S. trinitiensis* n. sp. is the larger size of P$\frac{4}{}$ and M$\frac{1}{}$ in the latter. This would place the Dallas specimen farther from *S. fatalis* than the California type.

Lull, aware of confusion that can be caused in the literature by too many species based on material too fragmentary in nature, placed the Dallas cranium with *S. fatalis* merely because both were from Texas and both were smaller than *S. californicus*. It could have just as well been referred to *S. nebrascensis*. Lull himself considered his identification provisional. In closing he says:

> "I have no assurance that the Dallas specimen is distinct from *S. fatalis*, with the proportions of which it approximately agrees. The discovery of a carnassial attached to the cranium in the Dallas sand pits alone can give assurance of identity or disagreement. Until then, this specimen must be referred provisionally to Leidy's species."

The present writer proposes that this specimen be referred to *S. trinitiensis* n. sp. on the basis of its closer physical, geological, and geographical affiliations.

Comparison with *S. floridanus*, Leidy

The cranium of *S. floridanus* (pl. 69, fig. 5) is almost as small as the Dallas specimen, but shares the wide rounded occipital feature of *S. californicus* (pl. 69, fig. 6). The postero-lateral area of the mastoid is smooth as in the new species, but in lateral view the mastoid process is almost vertical whereas the process in both *S. californicus* and *S. trinitiensis* n. sp. are distally inclined forward (pl. 69, fig. 3). Dentition and mandible are not known in the Florida type.

S. necator, Gervais

The new species, *S. trinitiensis*, is readily distinguished from the South American types by the extremely long diastemas of the latter.

Machaerodus gracilus, Cope and *M. mercerii*, Cope

All species of the sabre-tooth genus *Machaerodus* are distinguished by the presence of P3 which is absent in the Dallas mandible. There is also greater inferior development of the mandibular flange in *Machaerodus*.

Dinobastis serus, Cope

Comparison was made with a complete skull of *D. serus* through the courtesy of W. W. Newcomb, Jr., Texas Memorial Museum.

The shape of the occiput in *Dinobastis* superficially resembles the Dallas specimen, but the *Dinobastis* is larger and the mastoid and post-glenoid processes are widely separated. In this feature *Dinobastis* resembles true cats more closely. The mastoid and

post-glenoid processes are partially fused in *Smilodon*.

CONCLUSIONS

Both the Dallas mandible and the Dallas cranium display specialized traits that distinguish them from all comparable material. All three Dallas specimens are of almost identical geologic age. And though the theory of only one type occupying a single ecological niche at a given time is open to considerable question, it is the opinion of the writer that in view of the rarity of such material in this strata plus the fact that two of the specimens are specifically different from all species that are comparable, the cranium previously described as *S. fatalis* be referred to *S. trinitiensis* n. sp. as the first paratype.

LITERATURE CITED

ADAMS, G. L., 1896., The extinct Felidae of North America. Amer. Jour. Sci., ser. 4, v. 1, p. 419–444, pls. 10–12.

——, 1897, On the extinct Felidae. Amer. Jour. Sci., ser 4, v. 4, p. 145–149, figs. 4–8.

BOVARD, J. F., 1907, Notes on Quaternary Felidae from California. Univ. Calif. Publ. Bull. Dept. Geol., v. 5, p. 155–170, pls. 13–14.

BROWN, B., 1908., The Conard fissure, A Pleistocene bone deposit in northern Arkansas: With descriptions of two new genera and twenty new species of mammals. Mem. Amer. Mus. Nat., Hist., v. 9, pt. 4, p. 155–208, pls. 14–25.

COPE, E. D., 1880., On the extinct cats of America. Am. naturalist, v. 14, p. 833–858, 15 figs.

——, 1893., A new Pleistocene sabre-tooth. *Ibid.*, v. 27, p. 896–897.

——, 1894., Extinct Bovidae Canidae, and Felidae from the Pleistocene of the Plains. Jour. Acad. Nat. Sci. Phila., ser. 2, v. 9, p. 453–459, pls. 21–22.

——, 1895., The fossil vertebrata from the fissure at Port Kennedy Pa. Proc. Acad. Nat. Sci. Phila., p. 446–450.

——, 1899., Vertebrate remains from Port Kennedy bone deposit. Jour. Acad. Nat. Sci. Phila., ser. 2, v. 11, p. 193–267, pls. 18–21.

CROOK, W. W., JR. & HARRIS, R. K., 1957., Hearths and artifacts of early man near Lewisville, Texas, and associated faunal material. Bull. Tex. Arch. Soc., v. 28.

EATON, G. F., 1922., John Day Felidae in the Marsh collection. Amer. Jour. Sci., ser. 5, v. 4, p. 425–452, 12 figs. in text.

LEIDY, J., 1868., Notice of some vertebrate remains from Harden Co., Texas, Proc. Acad. Nat. Sci. Phila., p. 174–176.

——, 1889., The sabre-tooth tiger of Florida. Proc. Acad. Nat. Sci., Phila., p. 29–31.

LULL, R. S., 1921, Fauna of the Dallas Sand Pits. Amer. Jour. Sci., ser. 5, v. 2, p. 159–176, 5 figs. in text.

MATTHEW, W. D., 1918, Contributions to the Snake Creek fauna with notes upon the Pleistocene of western Nebraska. American Museum expedition of 1916. Bull. Amer. Nat,. Hist., v. 28, p. 226–229.

MERRIAM, J. C. & STOCK, C., 1932, The Felidae of Rancho La Brea. Carnegie inst. pub. no. 422.

QUINN, J. H., 1957., Pleistocene Equidae of Texas. Univ. of Texas, Bull. Ec. Geol., Rept. of Investigations no. 33.

MANUSCRIPT RECEIVED FEBRUARY 4, 1959

(*Explanation of* PLATE 69 *on next page*)

EXPLANATION OF PLATE 69

FIG. *1*—*Smilodon trinitiensis* Slaughter, n. sp. Right lower jaw. D.P.S.C., Dallas Museum of Natural History, cat. no. 3.04-1s, holotype. ×½

2—*Smilodon californicus* Bovard. Right lower jaw. After Merriam and Stock (1932). ×½

3—*Smilodon trinitiensis* Slaughter, n. sp. Cranium, lateral view. D.P.S.C., Dallas Museum of Natural History, cat. no. 1.52-h, paratype. ×⅓, approx.

4—*Smilodon trinitiensis* Slaughter, n. sp. Cranium, occipital view. D.P.S.C., Dallas Museum of Natural History, cat. no. 1.52-h, paratype. ×⅓ approx.

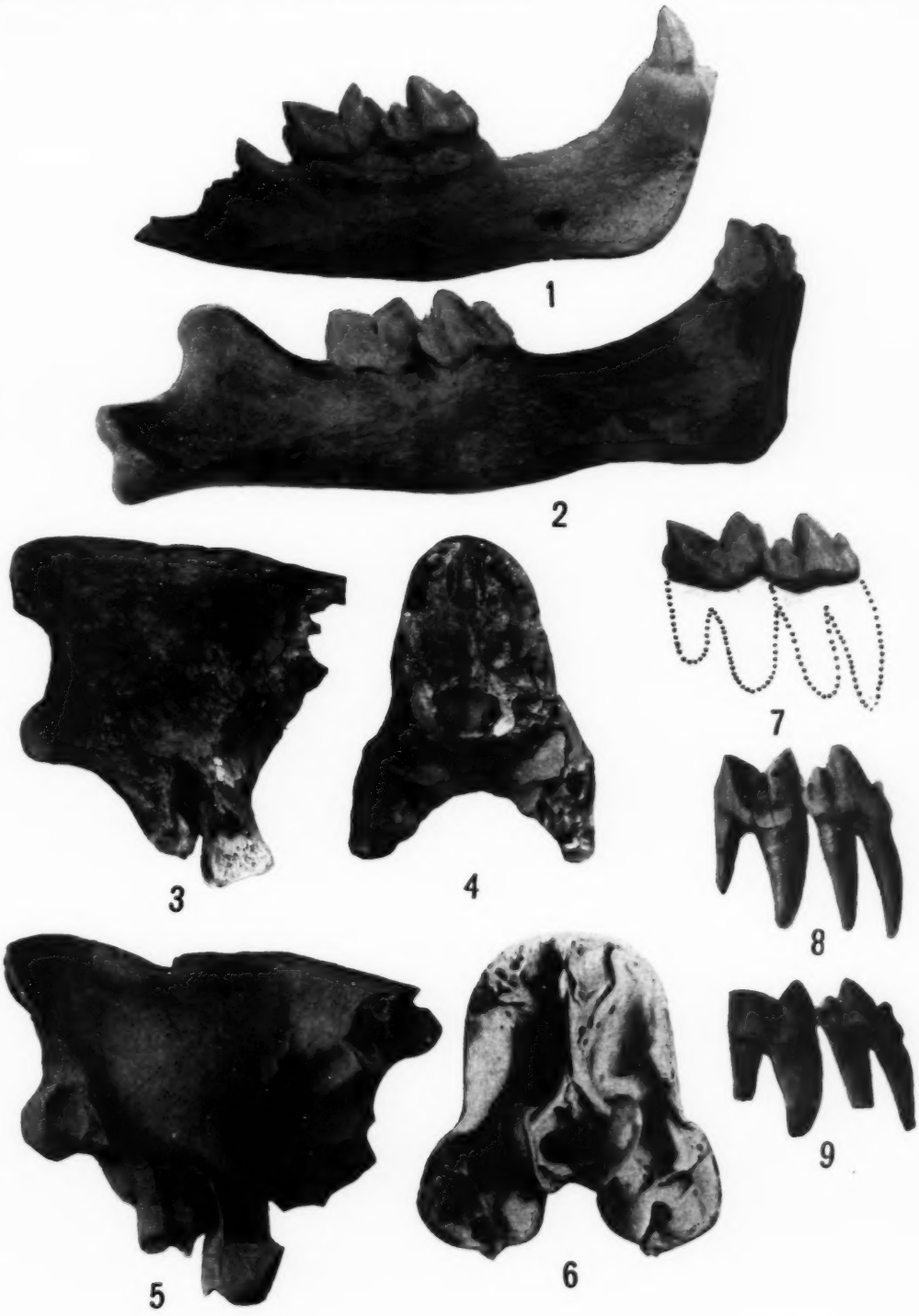
5—*Smilodon floridanus* Leidy. Cranium, lateral view. After Merriam and Stock (1932). ×⅓ approx.

6—*Smilodon californicus* Bovard. Cranium, occipital view. After Merriam and Stock (1932). ×⅓ approx.

7—*Smilodon trinitiensis* Slaughter, n. sp. P4 and M1. Roots restored from X-ray. ×½

8—*Smilodon californicus* Bovard. P4 and M1. After Merriam and Stock (1932). ×½

9—*Smilodontopsis troglodytes* Brown = *Smilodon troglodytes* (Brown). P4 and M1. After Brown (1908). ×½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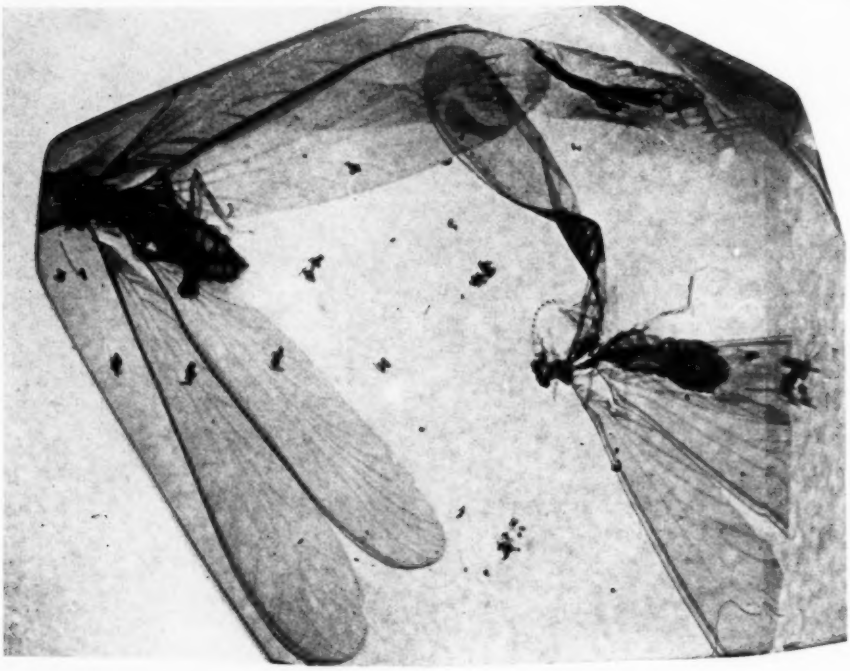

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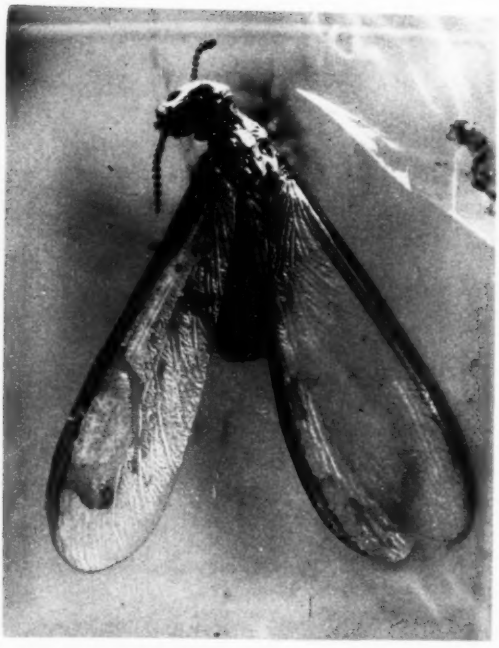

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JOURNAL OF PALEONTOLOGY v. 34, NO. 3, P. 493–494, PL. 70, MAY, 1960

FOSSIL TERMITES FROM TERTIARY AMBER OF CHIAPAS, MÉXICO (ISOPTERA)

THOMAS E. SNYDER
Smithsonian Institution, Washington, D. C.

ABSTRACT—A new fossil termite, *Heterotermes primaevus*, and a recent species, *Kalotermes nigritus* are recorded from amber of late Oligocene or early Miocene age from near Simojovel, Chiapas, México.

INTRODUCTION

EXAMINATION of four pieces of amber containing termites (Isoptera), from Chiapas, México has disclosed two species, one living today, and one new species. Both are in genera with species existing today in the same general area.

The fossil representing a living species is Univ. of California Paleo. No. 12613, from Simojovel area, Chiapas, México. It may be from any one of several localities ranging in age from Upper Oligocene to Middle Miocene. It is in the primitive family Kalotermitidae, and is a female winged adult of *Kalotermes nigritus* Snyder (fig. 3). This termite was described in 1946 from San José, Guatemala, Proc. Ent, Soc. Wash., vol. 48, No. 6, pp. 158–160. A small, dark colored species, it has also been found in México.

The following new species, in the family Rhinotermitidae, is described.

SYSTEMATIC PRESCRIPTION

HETEROTERMES PRIMAEVUS, n. sp.

Pl. 70, figs. 1–3

Winged adult.—Antenna light yellow-brown, 16 segments, pubescent, first segment elongate, cylindrical, next segments shorter, ring-like to wedge-shaped, becoming longer and elliptical towards apex.

Pronotum yellow-brown, subcordate, emarginate both anteriorly and posteriorly, with dense long hairs.

Wings smoky, costal veins yellow, margins of wings ciliate, surface punctate, with very dense hairs. In forewing cubitus and branches take up a larger area of the wing, reach the apex of the wing and there are 11 branches or sub-branches to lower margin of wing. In the Antillean *H. cardini* (Snyder) the cubitus is also closer to the subcostal vein than to the lower margin of the wing, which is not the case in *H. aureus* (Snyder) of California and Arizona, and western Mexico, or *H. convexinotatus* (Snyder) of the West Indies, Central and South America, or *H. maculatus* Light of western México. The median vein is closer to the cubitus than to the subcostal vein. In *H. crinutus* (Emerson) of British Guiana the median vein is intermediate and the cubitus in nearer to the lower margin of the wing. *H. tenuis* (Hagen) of the West Indies, Central and South America has the tissue of the wing less hairy.

Legs yellow, pubescent.

Tergites yellow-brown, with dense long hairs.

Measurements.

Length of entire winged adult	8.75 mm.
Length of entire dealated adult	3.50 mm.
Length of pronotum (where longest)	0.50 mm.
Length of hind tibia	0.83 mm.
Length of anterior wing	8.00 mm.
Width of pronotum	0.72 mm.
Width of anterior wing	2.50 mm.

EXPLANATION OF PLATE 70

FIGS. *1,2*—*Heterotermes primaevus*, n. sp. *1*, Dorsal view of holotype (Univ. Calif. Mus. Paleo. No. 12679a) on right and paratype (Univ. Calif. Mus. Paleo. No. 12679b) on left, ×8; *2*, enlargement (×9) of specimen 12679a, *3*, *Kalotermes nigritus* Snyder, dorsal view (Univ. Calif. Mus. Paleo. No. 12613)×10

Close to *H. cardini*, but tissue of wing in this Antillean species has but few hairs, whereas *primaevus* is densely hairy. It is larger than *H. hartungi* (Heer), a fossil from the Upper Miocene of Croatia.

Type material: Holotype (Univ. Calif. Mus. Paleo. no. 12679a) and two paratypes (Univ. Calif. Mus. Paleo. nos. 12679b and 12680) from same piece of amber, Univ. Calif. Mus. Paleo. loc. B-5103. Paratype 12680 has been deposited in the U. S. National Museum. An additional paratype (Univ. Calif. Mus. Paleo. no. 12637) is from purchased material from the Simojovel area and may be from any one of several localities ranging in age from upper Oligocene to middle Miocene. Loc.B5103 is from Las Cruces landslide, about 23 kms. (airline) south of east from town of Simojovel, and about 6.8 kms. southeast of the ranchhouse of Rancho Santo Domingo. The landslide is on the south slope of the major ridge locally known as Nichcalan (also known as Cerro Balumtum), near its southeast end, and about 1.4 km. northwest of Rancho San José Buena Vista. The amber was found in a sandstone exposed near the base of the western edge of slide. The marine invertebrate fauna from the adjacent beds indicates an age in the range from late Oligocene to early Miocene.

Described from the winged adult (fig. 2) except length of forewing measured from paratype in same piece of amber (fig. 1).

ACKNOWLEDGMENTS

Acknowledgment is made to the Associates in Tropical Biogeography of the University of California who have supported the field explorations and acquisition of the Chiapas amber, and to J. Wyatt Durham of the Museum of Paleontology, and P. D. Hurd, Jr. and Ray F. Smith of the Department of Entomology and Parasitology, University of California, who have made this fossil material available for study.

JOURNAL OF PALEONTOLOGY, V. 34, NO. 3, P. 495–496, 1 TEXT-FIG., May, 1960

A FOSSIL BRACONID WASP OF THE GENUS *ECPHYLUS* (HYMENOPTERA)

C. F. W. MUESEBECK
United States National Museum

ABSTRACT—A braconid wasp, *Ecphylus oculatus* n. sp. the first known fossil of this genus is described from amber of late Oligocene or early Miocene age from near Simojovel, Chiapas, México.

INTRODUCTION

A NEW species of braconid wasp was obtained from amber deposits in the State of Chiapas, México. The only known specimen is not in good condition; but I have prepared a description of it since it is the first known fossil specimen of the genus *Ecphylus*. Actually the living forms of this genus have been little studied and most of them also appear to be still undescribed. From available information it would seem that all species are parasitic on the larvae of certain wood-inhabiting Coleoptera, especially Scolytidae.

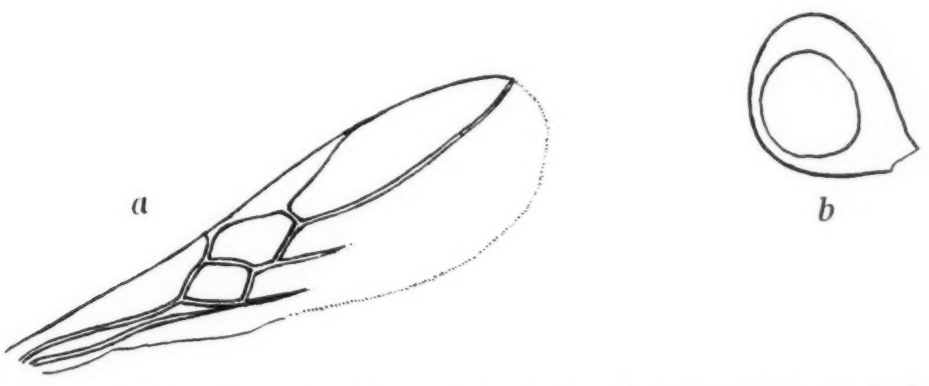
SYSTEMATIC DESCRIPTION

ECPHYLUS OCULATUS, n. sp.

The type, a damaged female, is a tiny specimen measuring only 1.2 mm. in length. It has exceptionally large eyes for a species of *Ecphylus* and the cubitus of the anterior wing is more strongly developed than is usually the case in this genus.

Head large, subquadrate; eye at least twice as wide as temple; antennae broken, only five segments of flagellum remaining, these very slender and the first a little shorter than the second. Lateral face of pronotum and the mesopleuron smooth and shining; anterior wing with radial cell attaining apex of wing; second abscissa of radius nearly straight; the first abscissa subequal with petiole of first discoidal cell and a little longer than intercubitus, the latter less than twice as long as second abscissa of cubitus; last abscissa of cubitus well developed and strongly pigmented for more than one-third the distance to the wing margin. Abdomen badly damaged and the ovipositor largely destroyed; first tergite longitudinally striate, the submedian keels strongly developed; remainder of dorsum of abdomen smooth.

Black; antennae dark; palpi pale yellow; wings subhyaline; legs brownish yellow; abdomen brownish piceous beyond the first tergite which is black.



TEXT-FIG. 1—*Ecphylus oculatus*, new species: *a*, anterior wing; *b*, outline of head, lateral view, showing unusually large eye, ×40

Type material: Holotype, Univ. Calif. Mus. Paleo. no. 12681, from loc. B-5103, Las Cruces landslide, Chiapas, México. The locality is about 23 kms. (airline) south of east from town of Simojovel and about 6.8 kms. southeast of the headquarters of the Rancho Santo Domingo. The landslide is on the south slope, near the southeast end, of the major ridge known locally as Nichcalan (also as Cerro Balumtum), and about 1.4 km. northwest of Rancho San José Buena Vista. The amber was found in a sandstone, exposed near the base of the western edge of slide. The marine invertebrate fauna from the adjacent beds indicates an age in the range from late Oligocene to early Miocene.

ACKNOWLEDGMENTS

Acknowledgment is made to the Associates in Tropical Biogeography of the University of California who have supported the field explorations and acquisition of the Chiapas amber, and to J. Wyatt Durham of the Museum of Paleontology, and P. D. Hurd, Jr. and Ray F. Smith of the Department of Entomology and Parasitology, University of California, who have made this fossil material available for study.

JOURNAL OF PALEONTOLOGY, V. 34, NO. 3, P. 497–539, 6 TEXT-FIGS., MAY, 1960

OUTLINE OF A THEORY OF ORIGIN OF THE VERTEBRATE

FRANK RAW, D.Sc., F.G.S.
Formerly lecturer in Geology, University of Birmingham, England

ABSTRACT—Vertebrates are derived from a very primitive Precambrian marine arthropod, the stage before compound eyes were evolved. Vertebrates arose from its free-swimming larval stage, and their organs evolved, through those of the prot arthropod, from those of the annelid. The evolution and deployment of the lower fishes (s.l.) are sketched. The first vertebrates evolved mainly in fresh water within one or more river basins of perhaps a "North-Atlantic" continent, though before this their ancestors were marine.

Through feeding on what floated down the streams to them, and learning to maintain their position against the current, the ancestors of the fish improved their ability to swim; by the time they reached the upland lakes, they were expert swimmers and might well be called fish. Becoming independent of the bottom except for rest, they swam near the surface, subsisting largely on floating food. Stimulated by this and by the light also from above, their complex ectodermal nervous system (perhaps 3 pairs of cords) migrated toward the mid-dorsal line, where overfolding from each side originated the tubular nerve cord.

Concomitantly, on the ventral side, with the increasing speed of swimming, the prot-arthropod mode of feeding was replaced by the chordate mode. The forward transport of food towards the mouth along the food groove between the two rows of appendages slowed down; and the food groove acquired digestive functions. Ultimately, all food was received in front, passed back along the food groove, and was digested in it. The arthropod gut was thus superseded and was absorbed. The arthropodan appendages of each segment coalesced ventrally to form a new gut and a new ventral body wall. Appendage-parts thus became gill arches, whereas the gaps between them formed the so-called "gill-slits," except that an anterior and a posterior gap formed respectively the new mouth and the new anus.

Further efficiency in swimming was effected when turgid cells along the top of the food groove acted as an elastic rod, became completely ensheathed in connective tissue and formed the notochord. Further, since with more rapid swimming fewer gills were needed, the partings between the gill arches, from behind forwards, progressively closed, and the sections of body cavity within the gill arches became united to form the splanchnocoel. Thus arose a new gut and new ventral body-wall.

Many peculiarities find their explanation in this theory: the vertebrate eyes acquired their character by the neural overfolds above mentioned and are traceable, together with the 4-fold pineal eye of primitive vertebrates back to the polychaete; the jaws are derived from an anterior pair of the prot-arthropod appendages, the upper jaw from their proximal, the lower from their distal parts; the vertebrate limbs, originating as fins, arose, each from a group of prot-arthropod pleura, which are appendage parts, traceable back to the polychaete, and were still moved by muscles. Further, the pectoral and pelvic arches originated, each from a group of gill-arches, and hence from groups of appendages of the prot-arthropod.

The fish evolved before Cambrian time. But the course of its evolution can be determined, because its detailed effects are seen in the structures and tissues inherited by fossil and modern forms.

INTRODUCTION

THE origin by evolution of the phyla of animals and plants is now accepted, but within every phylum the evidence for the successive stages is very incomplete. The range of size and complexity among modern forms of life, both animals and plants, is tremendous. Animals range from single-celled organisms to man and other vertebrates; and a similar range of complexity obtains also in the ontogenies.

The morphology, comparative anatomy and ontogeny of organisms furnishes much which is accepted as evidence of their evolution. To this can be added the evidence from the fossil record. But fossils are largely limited to the skeletons of those creatures which had them. Hence only very inadequately do fossils represent the life of the past. The early history of life must have been successions of creatures without durable skeletons. It is partly for this reason

that Precambrian rocks are practically without fossils, thus giving us little evidence of the life of the time.

The fossil record to the base of the Cambrian rocks is estimated to extend over a period of about 500 million years; but it is confidently deduced that the earlier unrecorded life period was very much longer. Here it is assumed to be not less than 2000 million years. For, though we do not find vertebrate fossils extending down to the base of the Cambrian, nevertheless, from the position and character of the oldest of them, we can feel confident that vertebrates were already present in the Cambrian period. And if, during the fossil record, modern vertebrates have been evolved from Cambrian fish, how much longer a period shall be assigned to the evolution of those fish from the first life on the earth?

The origin of the vertebrate is something we shall never see represented by fossils. It must be deduced from what we see in living forms, supplemented by the fossil record.

During the last century and this, many different theories of the origin of the vertebrate have been advanced. But, at the present time, practically all modern zoological text-books accept a close relationship of the vertebrate to echinoderms through the tunicates; though few authorities would claim that this origin has been proved.

The writer is unable to accept this supposed relationship of the vertebrates to the echinoderms and their descent through the tunicates. On the contrary, he considers that the vertebrates have been derived from higher marine worms through the ancestors of the arthropods, and that the tunicates are degenerate. It is therefore the purpose of this paper to present the evidence for this view, which is developed in detail and as briefly as possible.

For his facts the writer is mostly indebted to others, since his own research has mainly been on the trilobites. But as his studies led back to the polychaete and from them back to the primitive annelid, so they led also forward to various arthropods, and forward also to primitive vertebrates represented by early Palaeozoic fossils. For illustrations of these in text-figures 3,4,5 and 6, the author is indebted to Dr. Anatol Heintz, Professor of Palaeontology in Oslo University.

1. TWELVE PRINCIPLES OF MORPHOLOGY, EMBRYOLOGY AND EVOLUTION INVOLVED

As the views here expressed are in such marked contrast with those which have held the field for the last half century and more, and as they seem to violate principles which have been accepted as biological laws, some discussion of principles seems desirable. Below are submitted 12 principles which in the writer's view are involved in this major evolution. The idea is due to Prof. G. F. Ferris of Stanford University, California, who in his "Microentomology" (1948) enunciated 6 principles of Comparative Morphology applicable to the study of the Annulata. These need not be given here; the writer will state his views where he disagrees with Ferris.

Principle I. Time is a very important factor in evolution.

This principle has been too little considered by zoologists. Life on the earth is extremely old. It has probably existed for at least 2000 millions of years, i.e., four times as long as our fossil record. Prof. Arthur Holmes (1947) gave the figure 3350 million years for the age of the earth.

Most of organic evolution, too, is extremely old. From the fossil record it is highly probable that all the great phyla of animals, including early fish, members of our own phylum, were evolved before Cambrian time, though the earliest of known "fishes," a specialised type, occurs in Middle Ordovician rocks (Colorado, Wyoming and South Dakota). We may therefore ask ourselves: if the evolution from early fish to man occupied 500 million years (the estimated duration of the record), how much time would be required for the evolution of the fish from a lower phylum, or indeed from the original life? Young, however (1950, p. 724), assigns only 500 million years to the whole chordate history.

Ferris states that "no morphologist would agree that he is a Lamarckian," that "Lamarckism does not lend itself to a consistent system of principles, but to the principle of disorder in evolution." Lamarck's 4th law (published in 1815) is, briefly, that acquired characters are inherited, but, following Weismann's lead, this law is not admitted by zoologists.

On the contrary we can state:

Principle II. Lamarckism seems an important factor in evolution, as important perhaps as Darwinian natural selection. It is difficult to see how evolution could have occurred without some degree of inheritance of acquired characters in geological time.

The course of evolution that we can trace is usually the same as the effects of activities and of use and disuse, and is so vast. Can one imagine, for example, the complex evolution of the elephant and giraffe by means of the natural selection of variations independent of habit? We should not refuse to consider the evidence, spread over millions of years, which the palaeontological record supplies (contrast, e.g., Young, 1950, p. 6).

Furthermore, Ferris postulates that "all evolutionary changes have arisen from changes in the genetic materials, and are transmitted only in accord with the laws of genetics, known or unknown" (see also Young, 1950, p. 22). This may well be; but what we need to know is, what causes the changes in the "genetic materials"?

On the contrary we can state:

Principle III. The directions of evolution are attributable mainly to external causes, i.e., *to the stimulus of the constantly changing environment.*

The environment is changing, often every moment, owing to motion of water or air, to variations in heat, light, and all the elements of the weather; furthermore, all the elements of the biological environment change every day, every year, etc. In fact such changes are astronomical, geographical, geological, biological. One may ask: are mutations independent of the external environment? Life has thus been constantly stimulated to spread to new fields, to seek new modes of making a living, or new foods, to find new modes of feeding, and so on.

Principle IV. Evolution has not only been very complex, but, for each organism it must have been in very many different directions at different times.

This is because the geographical and biological environment was so frequently changed by astronomical, geological and other causes.

Ferris postulates that "Evolution has been continuous and orderly, each change being based upon a stage that has gone before."

On the contrary one can state:

Principle V. The speeds of evolutionary change have varied so enormously, that evolution has been relatively discontinuous. Also, many of the changes have been largely independent of what had gone before.

In a previous paper (Raw, 1949) the writer has deduced that during its evolution the polychaet changed its mode of feeding three times over, with great effects on the brain and on the visceral nervous system; and in the evolution from this of the arthropod, the mode of feeding changed again. The abundant vestigial organs also suggest abrupt changes of habit, crises in evolution.

Principle VI. Organic evolution during 2000 million years (Principle I) has been so complicated and so long and varied that often very little of it can possibly be represented in the ontogeny.

Because evolution has been in so many different directions at different times, any ontogenetic representation of it is bound to be full of short-cuts and compromises. Furthermore, the successive stages of embryo and larva had to live under quite different conditions from those of successive ancestors, and therefore cannot closely resemble them. Hence, only a limited reliance can be placed upon the phylogenetic interpretation of ontogeny. That this is so in the Chordata, has lately been claimed by H. Barraclough Fell (1949), who has pointed out how extremely varied are the larvae within the Echinodermata. Young (1950, p. 48) does not mention Fell's paper, but relies on a similarity of development processes. The varied nature of the echinoderm larvae suggests that comparative anatomy may in many cases be more reliable than is ontogeny for indicating the course of evolution. In general only the latest stages of the ontogeny give precise indications of the phylogeny. The facts of palaeontology, however, are strongly in support of the value of ontogeny for indicating phylogeny.

All higher creatures have evolved, it is believed, from primitive unicellular life, and all individuals begin their lives as single cells. We may note also that in the ontogeny of segmented animals, the segments are successively added. Very erroneous views have been based on this last fact. It has, for example, been claimed that the arthropod

was directly derived from an unsegmented worm, and that the segmentation had arisen anew in the arthropod. Bateson (1886) and several others, including Young (1950) and Berrill (1955), have considered the chordate as derivable directly from an unsegmented creature.

Principle VII. In evolution, nature is ever adapting old organs to new uses, rather than inventing new organs. We should therefore look for the origins of the organs of higher animals in those of lower creatures, rather than attribute them to a new origin.

It is claimed, for example, by those holding the current view, that *within* the vertebrate phylum the segmentation, sense organs, brain, gill-arches, gills, "gill-slits," and fins have all arisen anew; whereas the writer would derive all of these except the dorsal fins from organs of the invertebrate ancestor. On this latter view, the segmentation of the annelid, the arthropod and the vertebrate *is one and the same.* After it arose, there were always segmented animals to adopt new modes of life; and they have dominated the earth ever since.

Principle VIII. Within this great superphylum, for which the term Segmentata is here suggested, the anterior pole for locomotion and for feeding has been constant, and this has led to great cephalisation.

This cephalisation in the polychaete has been deduced by the writer (1949), who claimed it to be very complex and to involve much of the anterior part of the body of the primitive annelid. To this polychaete head has been added further cephalisation in the evolution of the arthropod, which involved much of the anterior part of the polychaete (Raw, 1953). Yet again, in the evolution of the vertebrate, a further variable cephalisation has occurred, beyond that which was present in the earliest arthropod —the prot-arthropod. This vertebrate cephalisation had already reached very advanced but varied stages in the earliest of known "fishes" (s.l.) (Osteostraci, Anaspida, Heterostraci, Placodermi), but all these became extinct.

Principle IX. Owing to cephalisation the least evolved part of the bodies of all the Segmentata is the post-cephalic part, not the head.

Principle X. The course of evolution is not reversible.

Even when a return to a previously discarded habitat and mode of life has occurred, the old body is not regained, and numerous vestigial organs remain to indicate the phylogenetic history.

Principle XI. Intensive study of the origin of the vertebrate strongly suggests that the destinies of the germinal layers, supposedly immutable, have not remained fixed, but have been subject to extensive evolution within the phylum.

Within this phylum, as deduced below, both the dorsal and ventral surfaces (ectoderm) inherited from the invertebrate ancestor became internal, and have become respectively the tubular nerve cord and the gut; but, whereas the first has long been recognised as an ectodermal product, the second is erroneously claimed as the same endoderm as that of lower phyla.

On the contrary, if the conclusions claimed below are accepted, it will be agreed that the gastrula of the chordate, e.g., of *Amphioxus*, is a quite different and later one than that of lower phyla. Thus Haeckel's simple "gastraea theory" does not apply to the vertebrates; and the "chordula," which in their ontogeny follows the gastrula, does not closely resemble an ancestor.

The duration of the ontogeny of a creature is as nothing in comparison with that of its phylogeny, and hence cannot possibly represent the latter in detail; and in the vertebrate a large early section is unrepresented.

Principle XII. The great extent of the evolution that has taken place within the various phyla has not yet been realised.

It is this, the writer believes, which has largely blocked advance in tracing the relationships between them. Vertebrates are not derived from annelids or from arthropods because of the great contrasts existing between their modern representations and vertebrates. But if one fully appreciates the amount of evolution that has occurred within each, he will realise that the contrasts were formerly very much less (e.g., in Precambrian time).

2. PREVIOUS THEORIES OF ORIGIN OF THE VERTEBRATES

Since the general acceptance of the doctrine of evolution, theories of origin of the

TABLE 1.—PREVIOUS THEORIES OF ORIGIN OF THE VERTEBRATES

Theoretical Ancestor	Author	Date
1. Arthropod dorso-ventrally reversed		
Generalized arthropod	G. St. Hilaire	1822
	F. Leydig	1864
Merostome	W. Patten	1890–1912
2. Tunicate (ascidian)	A. Kowalewsky	1866
3. Annelid dorso-ventrally reversed	A. Dohrn	1875
	C. Semper	1875
	H. Eisig	1887
	C. S. Minot	1897
	E. Perrier	1898
	H. C. Delsman	1913, 1922
	J. G. Kerr	1919, 1945
4. Lower worm not dorso-ventrally reversed		
Annelid	F. M. Balfour	1878
Nemertean	A. A. W. Hubrecht	1883
	A. Haeckel	1903
	E. R. Lankester	1910
Turbellarian	A. Goette	1884, 1895
5. Arthropod (near merostome) not reversed	W. H. Gaskell	1889–1908
6. Enteropneust, and this from an echinoderm	W. Bateson	1886
7. Pelagic tunicate, and this from an echinoderm		
From a pelagic echinoderm larva	A. Willey	1894
	W. Garstang	1894, 1945
	W. K. Gregory	1936, 1950
	G. R. deBeer	1938
	A. Heintz	1939
Pelagic tunicate (cf. *Appendicularia* larva)	W. K. Brooks	1893
Pelagic larva of ascidian tunicate, became neotenous, ascending rivers to feed, returning to sea to breed, later evolved in rivers into ostracoderm	N. J. Berrill	1955
8. Sessile tunicate, and this from a pelmatozoan echinoderm, but with larva like the holothurian "*Auricularia*"	J. Z. Young	1950
9. Pelagic cerianthid coelenterate	A. Lamerre	1891–1905

vertebrates have been advanced in considerable number; but none has met with universal acceptance, because none has appeared fully reasonable. Hence the origin of this phylum still remains one of the greatest problems in phylogeny. Indeed no completely new theory seems to have appeared within the present century, the reason for which is doubtless the great contrast in organisation, structure and bodily activities between the chordates and all non-chordates and the fact that no one has been able to make sufficiently close comparisons.

The profuse segmentation of primitive vertebrates led early last century to the theory that they must have arisen from richly segmented invertebrates such as arthropods or annelids. On the other hand, Bateson later (1886) supposed that segmentation had arisen within the phylum, and so also did Willey (1894) and others, including modern writers, such as J. Z. Young (1950) and N. J. Berrill (1955).

The nature of the contrast between articulates and vertebrates led the earlier theorists to suppose that the segmented invertebrate had become inverted to originate the vertebrate. Although this was indeed claimed by Patten as late as 1912, the theory has proved very difficult to accept.

Table 1 lists the various theories known to the writer. The order in which they stand is roughly that of their introduction, but only within each group are the names of authors in chronological order. As indicated in the table, the theories may be divided into 9 groups.

For the most part, detailed comparisons have not been made between the organs and structures of chordates and those of their supposed non-chordate ancestors. As shown below, however, Gaskell went further than

many workers in this direction. These comparisons are often so weak that several authors have not even appreciated the difference between reversal and non-reversal of the supposed ancestral articulate. C. S. Minot, for example (1897), accepts the Dohrn-Senper theory, without referring to the dorso-ventral maintenance or reversal; in reviewing the theories of Gaskell and of Patten he never refers to it, although Gaskell's comparison is with the merostome *without reversal*, whereas Patten's is with the same, but *with reversal*. Perrier (1898) and Young (1950, p. 47) also put these two together as the same. Further, Minot and several others, including Young, offer no explanation whatever of the tubular central cord, the gill-slits, the gill arches, the notochord or the appendages.

The opinion usually expressed of relationship of the vertebrates to echinoderms has now been current for more than half a century, but it has not brought zoologists any nearer to a realisation of the origin of the peculiarities of the vertebrate organisation. Most of those who have espoused it must have realised how inadequate it was, for none has made a serious attempt at explanation. But now that such great advance has been made in vertebrate palaeontology among the older fossiliferous systems, zoologists should not ignore phylogeny, as they frequently do; for the comparative anatomy of the recent and the fossil together with ontogeny furnish evidence for definite conclusions as to the origin of all the higher phyla. In a similar category is the derivation of the vertebrate from the enteropneust or from a tunicate, for both are degenerate, not progressive, creatures.

To deduce the vertebrate ancestry it is obviously necessary to study the earliest fossil members and the best representatives of these. The earliest are of Ordovician and Silurian age, but these are very fragmentary and have evidently been transported; it is probable that none of them lived where their remains are found. The earliest that are entombed in deposits of their own habitat are of Devonian age and are found in the lake deposits of the Old Red Sandstone. Many are complete and well preserved and are clearly freshwater forms.

3. RELATIONS OF THE VERTEBRATE TO THE POLYCHAET AND THE PROT-ARTHROPOD

The derivation of the vertebrate is, the writer believes, from the prot-arthropod without dorso-ventral reversal; and hence also from the polychaete without reversal. This needs amplification. Study of trilobites has furnished many ideas. They are not Crustacea. By themselves they constitute much the most primitive of the known classes of arthropods. Their characteristics suggest the origin of the arthropod from a particular type of polychaete which had characteristics of the Eunicidae, the Phyllodocidae and the Polynoidae (Raw, 1953). Study of the Eunicidae led back to the origin of the polychaete (Raw, 1949) so that in a more recent paper (Raw, 1955) the following stages between the primitive annelid and the arthropod classes are defined:

1. Primitive annelid with brain limited to the "fore-brain," and without the extended prostomium, stomodeum and visceral nervous system of the polychaete; probably with segmental eyes.

2. Primitive polychaete (such as *Eunice*), its extended prostomium with brain enlarged by the addition of 3 pairs of segmental ganglia forming the mid-brain and also by the hind-brain pair of ganglia; and with stomodeum and visceral nervous system greatly extended.

3. Special polynoid polychaete, the ancestor of the arthropods; with periodicity of segmentation like the polynoid (cf. subfamilies Polynoina and Hermionina).

4. Pro-arthropod (suggested by adults and larvae of trilobites) with segmentation like an annelid but with a firm exoskeleton and biramous appendages throughout, behind an anterior pair of antennae.

5. Prot-arthropod (suggested by trilobites and the ontogenies of insects); like the last, but with the arthropod head evolved by the constant subretroversion of the prostomium and peristome in a new mode of feeding, whereby these parts and the following six segments coalesced into the head, which was furnished with 9 pairs of simple eyes segmental in origin.

6. Deut-arthropod (suggested by trilobites and other arthropods) with ventral eyes like the last, but also with dorsal compound eyes, each succeeding the six simple dorsal eyes of a side and developed along the new common nerve of the six.

Stages 1 to 5 of the above series were common both to arthropods and chordates, whereas Stage 6 is limited to arthropods. In the series there is no room for *Peripatus*. Comparison with the trilobite (1953, p. 82) shows that *Peripatus* is not an arthropod and therefore must not be called a prot-arthropod, as Sedgwick, Lankester, Kerr and others have done.

Much as study of the trilobite led back to the worm and from it forward to the various arthropod classes, so it led from the worm forward to the vertebrate, which is thought to have arisen from larval stages of an early prot-arthropod.

It may be considered that the contrast in composition of the skeleton in all the known arthropods and in the vertebrates rules out their association. But both annulates and vertebrates exhibit considerable variety in this, and it is clear that the skeleton has changed its nature in the course of evolution. The change of habitat of the evolving vertebrate from sea water to land water might be expected to have a great effect. Certainly, the change to a vertebrate from a primitive arthropod is much less drastic than would be that from an echinoderm.

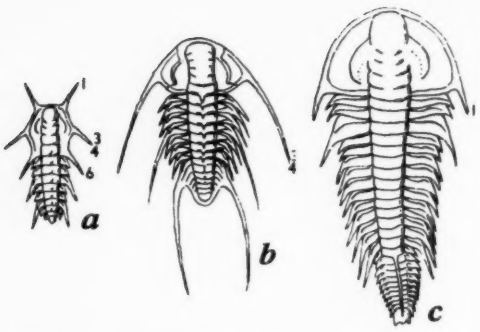
Of the many theories of origin of the vertebrate which have been advanced, few compare with this detailed below. First there is the view of F. W. Balfour (1878) who supposed that the primitive position of the nerve-cords of the annelid was lateral, and that they migrated ventrally in annelids but dorsally in the ancestor of vertebrates. The same principle was involved in the views of A. A. W. Hubrecht (1883) and Lankester that nemerteans had been the ancestor. But the unsegmented character of the Nemertea makes it unnecessary to consider them further. The only one who derived the vertebrate from an arthropod without reversal was W. H. Gaskell (1908), who however derived them from an advanced class comparable with a king crab or a eurypterid. Gaskell's views were scorned in his lifetime, and have been ignored since. Goodrich (1909, 1930), for example, and many others do not mention his work. But in the writer's view his theory helps to explain, better than any other, one of the great contrasts between the lower and the higher segmented animals, namely, the absence of gill slits in the alimentary canal of the one and their presence in the other. Gaskell was struck too by the contrast between the "solid" ventral nerve cords of the one and the tubular dorsal nerve cord of the other; and this also he made a valiant effort to explain.

4. INHERITANCE FROM THE POLYCHAETE AND PROT-ARTHROPOD

To the polychaete's "fore-brain," which in the author's view had been the brain of the primitive annelid, four pairs of segmental ganglia (representing at least three, but not consecutive segments) had been added to constitute the polychaete's brain or cephalic ganglia; and this has become so consolidated in advanced families that it has largely lost the evidence of segmentation (Raw, 1949). It was this complex brain of the polychaete which constituted the brain of the prot-arthropod, and in an inrolled form became the "fore-brain" of the vertebrate, but great evolution of the nervous system in both has taken place since.

From the annelid through the prot-arthropod the primitive vertebrate inherited its profuse segmentation, fore-brain, eyes, nerve-cords (which were then lateral in position and not limited to two), segmental nerves, a visceral nervous system, the originals of the limbs (viz., the pleura, which also are appendages, and in the vertebrate are seen most primitively in the ventrolateral "scales," so-called, of cephalaspids) and the gills. From the annelid it also inherited an extensively ciliated surface, part of which still survives (principle XII).

Studies of polychaetes, trilobites and other arthropods indicate that the prot-arthropod inherited its limbs and its eyes, which were simple, not compound, from the preceding stage, the pro-arthropod. The limbs were well developed and arthropodan in character (Raw, 1953) before the arthropod head was



TEXT-FIG. *1*. Trilobites in dorsal aspect, with primitive characters. All, as found, flattened by compression in shale. Six segments are coalesced in the dorsum of the head. Visual surface of eyes not seen; it coincides with the outer limit of the curved eye-lobe, and in life extended vertically beneath this.

a, *Olenelloides armatus* Peach. Lower Cambrian. An adult, though small. Head specialized by loss of suture and by forward eyes. The anterior apparent segment is actually double (as in fig. *c*). Thorax with macropleural macrosomites, as on head. Numbers beside the various spines are those of the dorsal macrosomite segments which bear them. In the pleural spines this and also *Albertella* (fig. *b*) are probably pelagic reversions (neotenic). After Peach, 1894, pl. 32.

b, *Albertella bosworthi* Walcott. Middle Cambrian. Primitive in regular segmentation of the head rachis and in extensive retention of axial spines. Of the paired head spines only the middle pair remain and in primitive position. Note segments coalesced in the pygidium. From Walcott, 1917, pl. 7, figs. 3, 3a.

c, *Olenellus vermontanus* (Hall). Lower Cambrian. Anterior head spines are here rotated to the rear, and are the only pair remaining. Anterior lobe of the head rachis (= first two dorsal segments) enlarged. Third post-cephalic has its pleura greatly enlarged and the 6th to some extent; both interpreted as macrosomites. Axial spines all lost except that on the 15th post-cephalic (a macrosomite), which is greatly specialized. Thorax exhibits secondary even development of pleura behind the 6th post-cephalic segment. This species is interpreted as an elongate reversion from a semi-ovoid *Olenellus*. It may be a male. From Walcott, 1910, pl. 26.

evolved, for they are practically the same on head, thorax and pygidium of the trilobite.

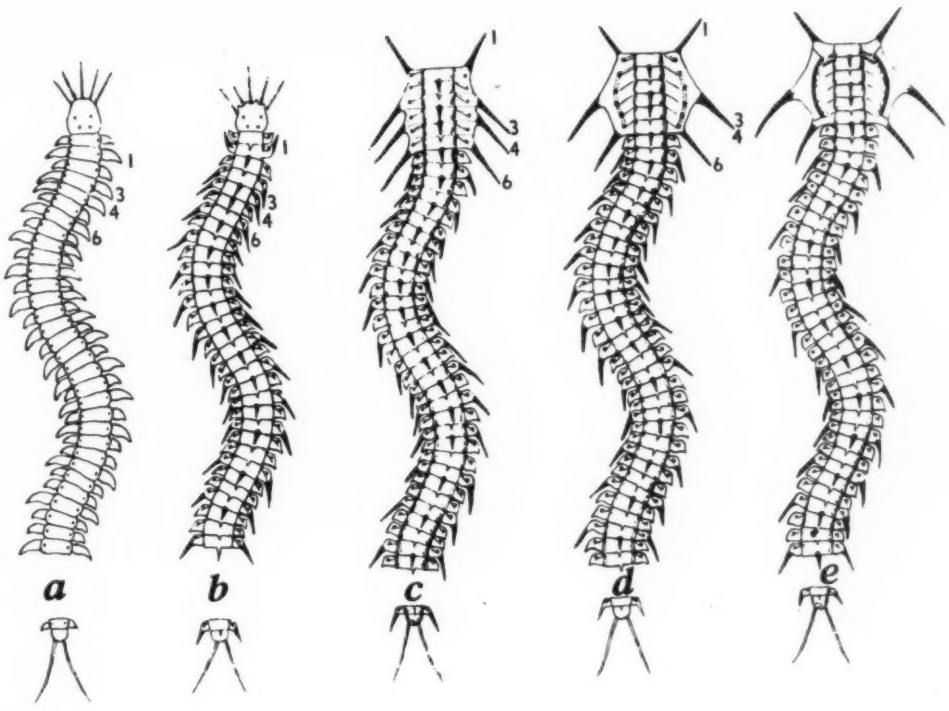
The arthropod originated by a new mode of feeding, probably from surfaces (Bernard, 1892; Raw, 1953). There was subretroversion of the prostomium and peristome of the pro-arthropod (derived from the polychaet), whereby more posterior appendages could serve the mouth. This led also to coalescence of the succeeding six terga and pleura, which formed a dorsal head shield under which were the subretroverted parts together with the appendages of all eight parts. This primitive arthropod head bore only simple eyes comprising two pairs from the prostomium, a pair from the peristome, and a pair belonging to each of the six dorsal segments (Raw, 1953). All these nine pairs of eyes are traceable in modern arthropods (see text-fig. *2a–e*) and three of them in vertebrates.

5. RELATIONS BETWEEN ARTHROPODS AND VERTEBRATES

Gaskell was right in claiming that the gill-arches with the gills represent arthropod appendages; and that the "gill-slits" are simply the gaps between them. This is supported by the recognised fact that the arches are segmental, whereas the "slits" are inter-segmental. The writer feels confident that no one who carefully studies the question can fail to agree with Gaskell in this. Gaskell believed that the vertebrate gills derived from "internally-situated branchiae," such as those present in Eurypterida; but this the writer cannot accept. On the contrary the appendages were very primitive.

That the gill-arches originated in appendages inherited from the prot-arthropod is a much simpler theory than that the gill-slits were developed *de novo* in the alimentary canal and body wall of the vertebrate (for which, besides, no explanation has ever been given).

Amphioxus, except for its anterior degeneration, is much the most primitive of existing Chordata, and strongly suggests that the gill-bars are appendages. Here, each primary gill-bar plus secondary or "tongue" bar represents a segmental appendage, which has lost its muscles, but still contains its extension of the body cavity; yet some zoologists are at pains to claim that each gill bar is covered on its inner surface with endoderm and on its outer with ectoderm (de Beer, 1928–45, p. 12). Both secrete parts of the internal skeleton, interpreted here as secreted at the inner boundary of what originally were ectoderm cells. It seems not



TEXT-FIG. 2. Stages in the evolution of the arthropod, from "The External Morphology of the Trilobite and its Significance," Raw, 1953, figs. 7A-E.

a, Ideal polychaet with notopodia like a phyllodocid (*Eteone*), segmental eye-spots as in a eunicid, and with merocyclism of a polynoid (Polynoinae and Hermioninae), the merocycles being diads to normal segment 22 and triads behind this.

b, Pro-arthropod suggested by trilobites, annelid-like in segmentation, but with terga of the whole protected by stronger cuticle and by axial spines. Two pairs of eyes on prostomium, a pair also on peristome, and segmental eyes on all segments presumably on the pleura. Notopodia are protective pleura, strengthened dorsally and ventrally, while being also appendages moved by muscles and bearing the pleural furrow. Neuropodia are legs and gills. Merocyclism exhibited by macrosomites bearing greater axial and pleural spines, which are blackened.

c, Early prot-arthropod. By habitual subretroversion of prostomium and peristome, these and the first 6 normal segments became the head. This originated by reduction of movement and concrescence of the adjoining pleura. It bore axial spines, and 4 pairs of lateral spines (on macrosomites 1, 3 and 4, and 6) in addition to 3 pairs of ventral eyes and 6 pairs of dorsal, which last were all innervated by their own segmental ganglia. The formation of the head originated the arthropod. Post-cephalic normal segments in merocycles, all bearing eyes; division between diads and triads may have become unstable.

d, Later prot-arthropod. Pleural spines on normal segments 3 and 4 on each side of the head have coalesced. Dorsal eyes have increased in size, and become innervated by way of the line of eyes and the nerves of an anterior pair. Enlargement of eyes and the new continuous light sensitive nerve along them caused the line of eyes to be a line of soft cuticle. Dorsal facial suture thus originated, the line of eyes becoming the ocular section whereas the anterior and posterior branches were partings between the 1st and last pleura and the free-cheek block between them (better seen in fig *c*). Prot-arthropod type of eyes recapitulated in larval development of many insects and in embryo of *Limulus*.

e, Deut-arthropod. Radiate eyes characterize trilobites and mandibulates, and at one time characterized chelicerates; all arthropods may have these eyes in their ancestry (possibly arachnids had them at one time and subsequently lost them). Merocylism represented as changed to that of the Olenellidae, triads beginning behind the head, as was the case also in the ancestor of the chelicerates, crustaceans and insects.

improbable that the successive elements of the branchial arches of the elasmobranch represent successive elements of the limbs of the prot-arthropod.

Gaskell believed that the vertebrate was derived from an arthropod approaching the arachnid in organisation. On the contrary, that it branched off from the appendiculate line very much earlier than this, is strongly suggested by *Amphioxus*, an undoubted chordate, where the gill-bars are cylinders of epidermis one cell thick, and the whole body is covered with an epidermis one cell thick; and, furthermore, the intestine and the atrium are ciliated throughout (A. Willey, 1910, p. 889). Also, the entire lack of any trace of compound eyes in the chordates suggests that they branched off before these organs evolved. For the fossil arthropods which were contemporary with the early fossil fishes, all likewise swimming aquatic creatures and comprising trilobites, eurypterids and crustaceans, were all possessed of compound eyes. Their absence in vertebrates, it is true, might be explained less satisfactorily by neoteny.

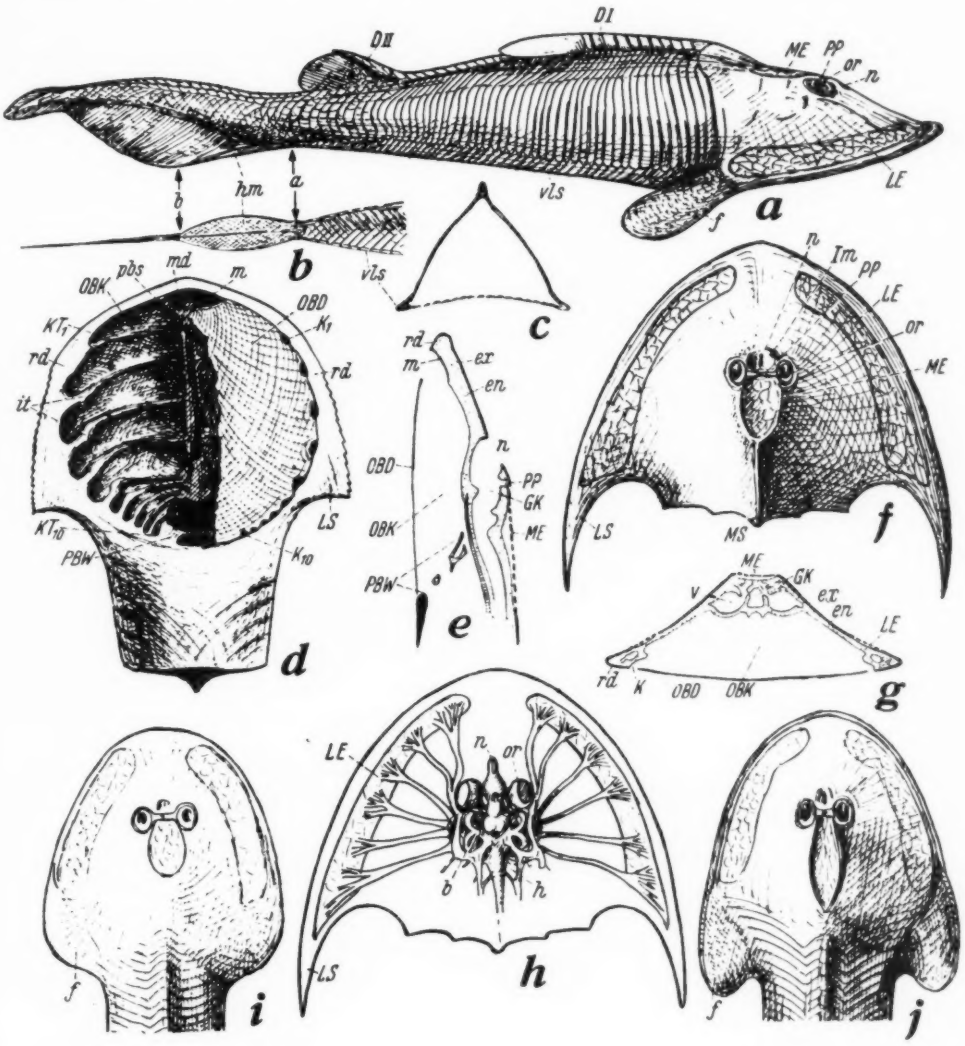
The same conclusion of derivation from the prot-arthropod may be drawn from further comparisons of the heads of arthropods and vertebrates; though it is in general impossible to recognise the boundary of the arthropod head in that of the vertebrate, unless it be in the cephalaspid, which in one respect is the most primitive of vertebrates, and which, besides, is extremely like a primitive arthropod but lacking ambulatory appendages. According to Stensiö (1927) the oral-branchial chamber under the head shield displays five larger gill pouches served by five large gill openings lying in front of the cornua (or head shield corners), followed by five smaller gill pouches served by smaller openings. It is accordingly possible to suppose that the five larger pouches belong to the equivalent of the arthropod head with its six normal segments and the following five to the first five segments of the succeeding many-segmented body of the prot-arthropod ancestor of the chordate. For this reason, as well as from the nature of the gill-arches in fishes, the prot-arthropod is indicated as the immediate ancestor.

In the way suggested above, the head of *Cephalaspis* is to some degree comparable with the head of a trilobite, which it so much resembles, due both to common inheritance of the head of the prot-arthropod and to convergence through similarity of habitat. And it may further be claimed that the compositions of the head shields is of the same character in each, namely, the coalesced terga and pleura of anterior segments (see text-fig. *3a–e*).

The six closely comparable nerves that according to Stensiö innervate each lateral sensory area of the head shield in cephalaspids strongly suggest the six dorsal segments of the trilobite cephalon (see text-fig. *3h*). The distribution of arteries and veins supports such an homology, though here as in the gills there seems to be a modification in front (see Stensiö, 1927, p. 136, 152,207,210,211,221).

If it should prove correct, that the heads of a primitive "fish," *Cephalaspis* and the most primitive arthropod, the trilobite, are to a degree homologous, it might furnish segmental correlation between arthropod and vertebrate. Stensiö was able to identify the foramina of the cranial nerves in *Cephalaspis* by their close correspondence with those of the lamprey; and, according to him, the anterior gill pouch is innervated by the profundus nerve, the 2nd by the trigeminal, the 3rd by the facial, the 4th by the glossopharyngeal, and the last large one, together with the small gill pouches, by branches of the vagus. The peculiar composition of the vagus, if it is due as here suggested to arthropod ancestry, would probably belong either to the last cephalic or to the first post-cephalic somite. And if, as seems most probable, the first of these alternatives is true, then the first gill of *Cephalaspis* would belong to the second dorsal segment of the arthropod, which equals the second somite behind the peristome of the polychaete; and the mandibular segment of the gnathostome would correspond to the third of these which is also the third in front of the occipital segment of the trilobite.

The primitive position of the vertebrate mouth is ventral; and in elasmobranchs and most lower fishes (s.l.) it remains so, though in Actinopterygii and the higher vertebrate classes it is terminal. On the view here developed the primitive position is inherited from the prot-arthropod, where the effec-



TEXT-FIG. 3. Cephalaspids. Mainly after Stensiö; All by kind permission from A. Heintz, 1938, p. 55, fig. 3.

a, Restoration of *Hemicyclaspis*, side view. *b*, Compound tail fin from below (after Heintz). *c*, Transverse section of body of same. *d*, Head shield of *Kiaeraspis* from below, the oralo-branchial cover partly removed to show the oralo-branchial chamber and gill pouches. *e*, Longitudinal section through head of *Cephalaspis*. *f*, Head of *Cephalaspis* from above. *g*, Cross-section of head of *Cephalaspis*. *h*, Restoration of brain capsule, lateral segmental sensory nerves and lateral sensory fields of *Cephalaspis*. *i*, Head of *Ateleaspis* (modified after Traquair). *j*, Head of *Aceraspis* (after Heintz).

Index to features on figures: a, anus; b, end of horizontal fin; b, (in H) semicircular canals; DI, DII, dorsal fins; en, endoskeleton; ex, exoskeleton; f, pectoral fin; GK, brain case; h, division for medulla oblongata; hm, horizontal membranous anal fin; Im, naso-hypophysial pit; it, inter-branchial septa; KI, KIO, 1st and last gill apertures; KT 1–10, gill pouches; LE, lateral sensory field; LS, lateral spine or cornu; m, mouth opening; md, upper surface of mouth; ME, median sensory field; n, nasso-hypophysial aperture; OBD, oralo-branchial cover; OBK, oralo-branchial chamber; or, orbit; pbs, pre-branchial ridge; PBW, post-branchial wall; PP, pineal plate; rd, ventral border of head-shield; v, otic capsule.

tive mouth is behind the base of the labrum (the sub-retroverted prostomium of the ancestral annelid). Covered (underlaid) by this labrum, the anterior appendages were modified and reduced.

6. OLD ALIMENTARY CANAL OF THE ARTHROPOD AND NEW CANAL OF THE VERTEBRATE

Since the gill-arches with their gills represent appendages, and the gill-"slits" the gaps between them, the whole pharynx is largely external to the body of the ancestor of the vertebrate, and constitutes a new or secondary alimentary canal, as Gaskell claimed.

But (1) the annelid has, and the primitive arthropod had, appendages on every normal segment of the body, (2) the pharynx in *Amphioxus* extends $\frac{2}{3}$ of the length of the body, and behind this the fin rays in the ventral fin are paired, supporting the suggestion that this ventral fin is indeed a coalescence of further pairs of appendages, and (3) in the vertebrate the whole alimentary canal is a unit extending ventral to the notochord. Therefore the whole canal is new, and originally was external. Also it probably originally extended the whole length of the body, and the anus was terminal.

The ancestral alimentary canal is therefore to be sought. Gaskell claimed that it is to be seen in the vesicles of the brain and in the spinal canal, and that only in this way could the unique tubular character of the vertebrate central nerve cord and the details of its form be explained. This explanation is opposed in the discussion below.

7. PROFUSE SEGMENTATION OF EARLY VERTEBRATES

Primitive Polychaeta can exhibit several hundreds of segments: the Trilobita, much the most primitive of known arthropods inherited profuse segmentation, some Cambrian forms exhibiting as many as 50 segments. The early fishes also, which are nearly all from fresh water deposits, exhibit great numbers of segments; for we can hardly doubt that the regular arrangement of their scales expresses the segmentation. The history of fishes shows great reduction of the number. The most primitive, the Anaspida, in Kiaer's careful restorations, have: in *Pharyngolepis oblongus* 186+; in *Pterolepis nitidus* 163+; and in *Rhyncholepis parvulus* 114+ segments—the figures given being counted behind the modified scales of the head in each case (see text-fig. *4a*). In the Cephalaspida, *Hemicyclaspis murchisoni* has 80 segments between the head and the base of the median tail fin (see text-fig. *3a*) and *Aceraspis robusta*, so far as they can be counted, has about the same number as *Hemicyclaspis*. Even these high figures probably represent great reduction in number. The tail also represents a further considerable number.

The elasmobranchs are very primitive among the gnathostomes, and they excel other groups in the number of segments.

Profuse segmentation can then be claimed as a primitive characteristic in vertebrates and points back to the polychaete and prot-arthropod.

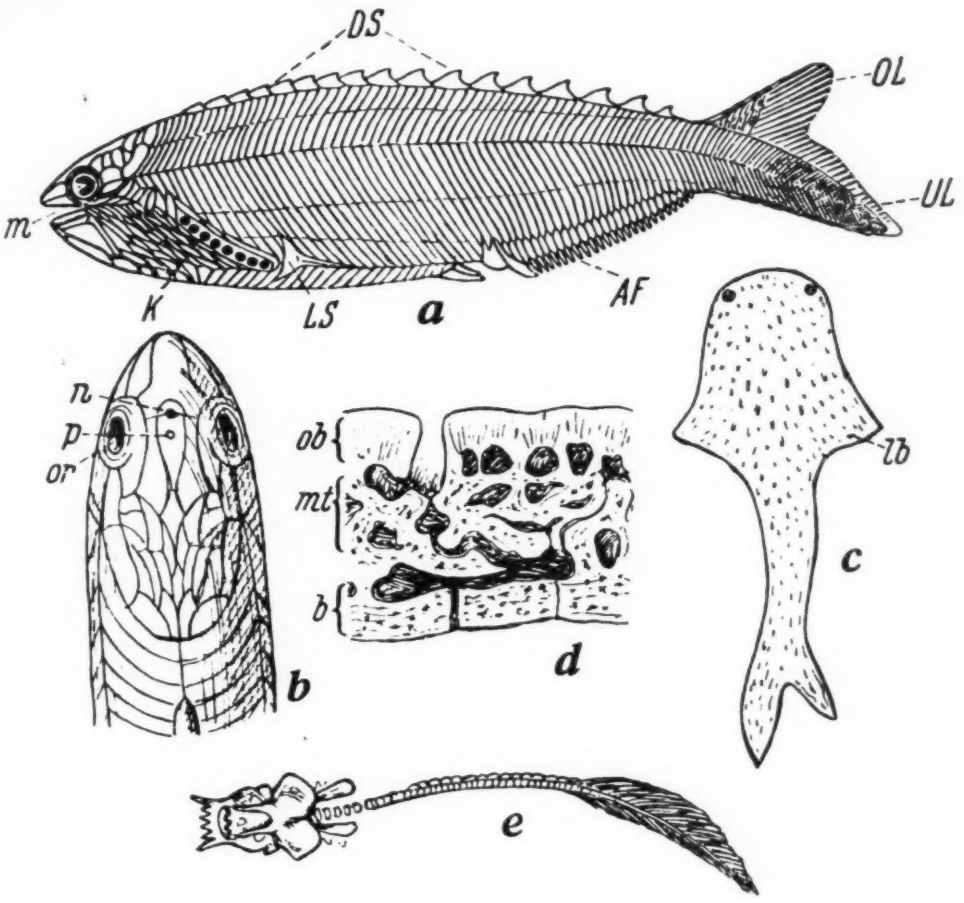
On the popular theory that the segmentation had to originate in the vertebrate, Young (1950, p. 28) suggests that it arose through the need for subdivision of the longitudinal musculature, so that it could serially contract for locomotion. Berrill also (1955, p. 168) discusses the origin of segmentation in his pelagic tunicate ancestor of the vertebrate. But the profuse segmentation in the earliest of known fishes is strongly against that view.

A reduction in the number of segments has been continued in certain fishes: in the most specialised Actinopterygians—the spiny teleosts—the numbers of distinct vertebrae has been reduced to less than 25.

8. DECISIVE FACTORS IN THE ORIGIN OF THE VERTEBRATE—DISTRIBUTION OF FOOD AND ITS ACQUISITION BY SWIMMING

To envisage the origin of the vertebrate phylum we must try to imagine the condition of life on the earth in and around the North-Atlantic continent several hundreds of millions of years ago. It was the environment of the rivers that originated the vertebrate, and it was mainly the development of swimming that shaped them.

The ancestor of the vertebrate was a much segmented marine pro- or prot-arthropod, and from this it has inherited its saline body fluids. It was a nectonic or pelagic larva be-



TEXT-FIG. 4. Some early vertebrates. All figures from A. Heintz, 1938, p. 57, fig. 4.
a, *Rhyncholepis*, an anaspid (after Kiaer). *b*, Head of same from above (after Kiaer). *c*, Restoration of *Thelodus* (after Traquair). *d*, Magnified cross-section of part of head-shield of *Cephalaspis* (after Stensiö). *e*, Restoration of *Palaeospondylus* (after Sollas and Bulman).
Features on figures: AF, anal fin; b, basal layer; DS, dorsal scutes; K, gill apertures; lb, lateral lobes; LS, lateral or pectoral spine; mt, middle layer; n, naso-hypophysial orifice; ob, outer layer: OL, upper lobe; or, orbit; p, pineal opening; UL, lower lobe.

fore becoming an ambulant adult. It is of great interest in this connection that the early larva of *Amphioxus* swims at the surface of the sea.

Vertebrate evolution probably began when the nectonic larvae discovered and began to feed on the microscopic food floating down the estuaries. They probably fed by a ciliary mechanism, using the food groove between the bases of the appendages, along which the food was carried forward to the mouth. Thence it was passed rearward through the arthropod gut.

There is much evidence that the immediate ancestor of the vertebrate was extensively ciliated. *Amphioxus* larvae are greatly ciliated, and the adult is ciliated from the mouth along the alimentary tract. Larval lampreys also "live by ciliary action for 3 or 4 years" (Regan, 1929). Thompson (1934) says from 3 to 5 years. In the course of its life it has two very different forms: first, an

ammocoete larva living for years on microscopic food and, second, after a metamorphosis which takes several months, a lamprey or *Petromyzon* which is carnivorous. The larval stage probably represents the more distant ancestor.

The great changes which marked the evolution of the vertebrate affected the whole organisation of the animal, down even to the germ plasm. They were correlated with the acquirement of more efficient swimming than any other group at that time possessed; and several of the changes probably took place concurrently. These changes, however, for their specification, we must separate, and several of them are discussed in the pages that follow. The ancestor could already swim, not only as the larva, but also as the adult, both by rhythmic lateral wave motion of the body, and by rhythmic motion of the foliate lobes of its appendages, like that in modern polychaetes. This it did in order to maintain its position against the river current. Swimming especially by lateral undulation, it thus secured the food before it was dispersed. It might be expected from their shape that the errant polychaetes would swim by undulations in the vertical plane. But their nerve cords were lateral in position, each controlling the muscles of its own side; and this would determine the lateral undulation. Of the two modes of swimming this was the one which persisted. As evolution gradually improved their speed, they were enabled finally to ascend the rivers, where the current was progressively stronger. Accordingly continually improving their speed, they would be relatively good swimmers by such time as they attained the still waters of the upland lakes. At the same time, as they ascended different rivers, and from these up various tributaries, they would meet a variety of biological and chemical conditions and would deploy into a variety of forms. It was their relative independence of the bottom that created the vertebrates. At first perhaps a larval exercise, swimming came to occupy more and more of the life cycle, and ultimately in the higher modern fishes practically the whole of it.

In striking contrast with this view are those of Young and Berrill. Young thinks he has "established" that the vertebrate originated either: (1) from a pelmatozoan echinoderm having a ciliated lophophore for food collecting and with a larva comparable with the auricularia of the Holothuroidea; thence through a sessile tunicate stage, whose free-swimming larva by neoteny gave rise to the fishes, which in his view first swam in the Palaeozoic seas (Young, 1950, p. 1,72); or (2) from the graptolites (p. 723).

Against the first view is the evidence to the contrary stated in this paper. Also against derivation from an echinoderm is the fact that in all echinoderms every ossicle of the skeleton is secreted as a single continuous crystal of calcite, and that this was already the case at the beginning of the palaeontological record as is known from Cambrian fossils of Shropshire and elsewhere. Furthermore, no echinoderm gives any promise of chordate structures.

Against Young's second suggestion is the fact that we know nothing of graptolites except they have an external chitinous sheath; they appear first in the Upper Cambrian, whereas already in Lower and Middle Ordovician highly evolved bony agnathous "fishes" existed (Bryant, 1936; Miller and others, 1947); and graptolites also give no suggestion of chordate structures,—only a similar branching of the chitinous sheaths to that of *Rhabdopleura*, a living pterobranch, the chordate affinities of which are disputed.

Berrill also describes in detail his view of the origin from a pelagic tunicate (1955, p. 119–199), but tunicates are best regarded as degenerates.

In contrast with our theory of the evolution of annelid and arthropod appendages into vertebrate swimming organs is the theory of origin by the subdivision of paired fin-folds, a pure invention. All the evidence advanced in support of the lateral fin-fold theory can be claimed as support for the annelid and prot-arthropod appendage theory.

In the anaspid, *Endiolepis aneri* described by Stensiö (1939) from the Upper Devonian of Scaumenac Bay, Canada, the long ventro-lateral fin-folds, perfectly divided into segments corresponding with the adjoining rows of body scales, suggest an origin in a segmental succession of appendages, though Stensiö derives it from a "paired fin-fold."

9. HISTORY OF THE NEW GUT

In furtherance of its swimming by

lateral undulations, the "arthropod" appendages of the ancestor would be held parallel to one another, and fairly close to the body so as not to impede the motion; also, in some of them at least, they were flexed in the middle like arms at the elbow, and in all cases the gills upon them effected respiration. This attitude, as regards the appendages, is indicated by the disposition of the gill arches in the Gnathostomata.

Of the appendages the antennae disappeared and some of the next appendages may have become modified or atrophied owing to being covered by the labrum,[1] but the succeeding pairs became united at their ends in the midline, where they met. In this way was formed a long ventral food basket and sieve, bounded at the sides by the appendages with partings between them; and so arose the gill-bars and "gill-slits," which latter are therefore quite wrongly named. So too was initiated a new body wall for the ventral half of the animal.

For a long time the prot-arthropod food groove would function, the food being carried *forward* along it to the mouth; but as the speed of swimming increased, this forward speed of transport of the food along it would diminish, at the same time that the cells of the food groove itself gradually acquired digestive functions, as Gaskell claimed. Moreover as this digestive function evolved, and swimming speed further increased, the forward motion of food to the old mouth finally ceased altogether, and was replaced by rearward motion through the "food-basket" bounded by the appendages with their gills, and by complete digestion along this tract. In such a way it is here claimed the new alimentary canal with its new mouth and anus must have originated, these apertures in both cases being originally gaps between adjacent pairs of appendages. The mouth is the foremost effective gap; but the anus probably owing to the special use of the tail as propeller and its great use also as rudder, may quite early have ceased to open at the end of the body, and may have shifted in a single stage to a position to the front of this organ. The fact that in the ontogeny of fishes a post-anal gut later disappears would thus receive its full explanation, for the food basket, which became the new gut, primitively extended the length of the body.

This is perhaps the only theory which attempts to explain the pecularities of the primitive vertebrate gut; and if it does this satisfactorily, thanks are due to Gaskell. For if he had not written his 1908 memoir, the present writer would probably never have attacked the problem.

10. THE BRAIN AND SPINAL CORD

The origin of the unique brain and spinal cord of the vertebrate is an outstanding problem of great importance and extreme interest. Gaskell claimed that the nerve cords had migrated on to the alimentary canal of the arthropod ancestor, the anterior expanded part of which formed, he thought, the vesicles of the brain, and the long intestine formed the spinal canal.

There are four reasons why Gaskell's theory is unacceptable:

I. Gaskell derived the vertebrate from a merostome-like "Palaeostracan," and he supposed that the nerve cords were already ventral and internal in position. The author's studies suggest, however, that the vertebrate branched off from the articulate very much earlier, as indicated above, and that, up to the time of completion of the polychaete's brain, the nerve cords were lateral in position, and still in the ectoderm. It is probable, too, that they were still in this condition in the prot-arthropod for the reasons that (1) they are still widely separated from one another in some modern Crustacea (e.g., *Apus*); (2) the embryology of the nervous system and of the eye in the vertebrates suggests that what has become the nerve cord was still part of the ectoderm, and that this was only a single cell thick, when the vertebrate spinal cord was first formed; and (3) in their ontogenies the movement of the neural folds towards the mid-line, where they coalesce, still suggests the migration of a pair (or pairs, see below) of nerve cords from previous lateral positions; notwithstanding that this migration must have occurred long before Cambrian time.

[1] In the writer's view this has taken place also in the arthropod. In the arachnida only the antennae have atrophied, and 6 pairs of appendages represent the 7 head "segments"; in the Crustacea, 5 pairs; and in the Insecta, 4 pairs of appendages represent the *same number* (7) of head "segments" (Raw, 1953).

II. The gut, inherited from the prot-arthropod, had previously hung in a central position in the body. Now, relieved of its alimentary functions, and superseded by another which lay ventrad of it, it tended to be relegated to a more dorsal position. But if, as Gaskell supposed, the nerve cords had settled on it, and if the neurocoele represented it, one would expect the neural folds in ontogeny in order to cover it to go under instead of only going over the neurocoele, as actually obtains. In other words, the neurocoele is by development an external space which is newly enclosed (Kerr, 1921, p. 327); not a previously internal space as was the old gut.

III. The very remarkable characteristics of the eyes of the vertebrate offer important evidence. The pineal and parapineal eyes have retinas which are normal, not being inverted, whereas the lateral eyes have the remarkable character that the retina is inverted. Light on reaching the latter first passes through the nerve fibres, rendered transparent, which are on their way to the optic nerve before reaching the sense cells themselves (Kerr, 1921, p. 340–342; 1919, p. 96–101).

The development and characteristics of these pineal and lateral eyes can be understood if we suppose that before the migration of lateral nerve cords towards the mid-dorsal line, the pineal eyes, primitively prostomial but now dorsal in position, were represented by two pairs of eyes near the mid-line, whereas the lateral eyes were represented by a pair farther apart from one another. A representation of the latter in the ontogeny of *Rana* is figured by Kerr (1919, p. 141) after Eycleshymer (1895). On the theory here developed the pineal and parapineal eyes represent the two pairs of prostomial eyes inherited from the polychaete, whereas the lateral eyes, also inherited from the same, are one of seven segmental pairs attributed by the writer to the head of the prot-arthropod. In the evolving chordate, a creature rapidly developing forward swimming, an anterior position for these eyes would constitute a great advantage, so that they were probably an anterior pair, belonging primitively either to the peristome or more probably to the following segment of the polychaete, the first dorsal segment of the primitive arthropod.

The pineal eyes already near to one another were probably still further approximated in the migration of the cords towards the mid-line and are not inverted; and the same applies to the parapineal. However, the lateral eyes were quite inverted by the movement, due probably to its rapidity and their own previous greater separation; and they have remained so, and have experienced a most remarkable evolution in their attainment of perfect vision. The distribution of these various eyes throughout the vertebrates suggest that the less modified pineal and parapineal largely served the ancestor till they were superseded by the much more efficient lateral eyes.

IV. There is nothing within the neurocoele to suggest the former presence of the gut; though this perhaps may be thought a poor argument in view of its apparent uselessness in such a position.

Both anatomy and embryology are thus definitely against Gaskell's view of this matter; and in the following discussion the writer offers what he hopes will prove the nucleus of a reasonable theory.

After such a tremendously long time the early stages of vertebrate evolution are difficult to determine, but on the writer's theory it had been preceded by the evolution of the polychaete and of the prot-arthropod. The polychaete had acquired a complex brain in the prostomium by the successive association of five pairs of ganglia, the first of which, the fore-brain, may itself have had a complex origin (Raw, 1949, p. 3). This brain innervated two pairs of eyes, which have become the pineal and parapineal of the vertebrate, besides other sense organs, of which the olfactory were handed on to the vertebrate.

In the evolution from this of the prot-arthropod the prostomium and peristome were subretroverted, and this would also involve the brain, which primitively would then form part of the labrum. But in modern arthropods inversion of the nervous system has been entirely removed because the brain has moved forward and upward in accordance with the migration of the prostomial eyes and the peristomial antennae. On the other hand, in the Vertebrata this has not been the case, for we still have a very marked cerebral flexure developed early in the ontogeny, which, in the writer's

view, is a recapitulation of the subretroversion of the brain in the origin of the arthropod. On this view the anterior limit of the primitive brain points rearward at the infundibulum. Balfour (1881, p. 266) offers a much less direct explanation.

The morphology of modern polychaetes strongly suggests that the primitive polychaete was characterised by sexneury having (1) a pair of nerve cords ventrolateral in position, which have become the ventral nerve cords of modern annelids and arthropods; (2) a pair of lateral or podial cords, still retained in the tetraneural families Amphinomidae and Euphrosynidae; and (3) a pair of dorsal or "nuchal" cords, still retained in the Spionidae, greatly developed and cephalised by the tetraneural families, and greatly reduced subsequently in other families (Raw, 1949, p. 25). It should be noted that the segmentally repeated nuchal organs of the primitive polychaete probably were ciliated as in modern polychaetes (Söderström, 1927).

The vertebrate arose very early, and the writer suggests that all three pairs of nerve cords were still present in the prot-arthropod ancestor, and that all three pairs of cords have united to produce the central nervous system of the vertebrate. That two have united is suggested by the uniform existence of dorsal and ventral roots. That there has been union of parts previously separated is suggested (1) by the structure of the spinal cord of *Amphioxus*, with its dorsal rift, and still more by that of the craniates with the dorsal and ventral fissures; (2) by the ontogenies, first, that of *Amphioxus*, where the ectoderm from each side grows over the medullary plate, and still more by the ontogenies of the craniates and other lower chordates where the neural folds move over and above the medullary plate to the mid-line so as to produce the neural canal. Further, that the medullary plate itself represents an earlier union of nerve cords than those of the neural folds is suggested by the fact that, although there is a ventral fissure in the spinal cord, the medullary plate is continuous across the median plane from its first appearance.

If the figures of Hatschek are reliable, *Amphioxus* does not exhibit typical neural folds. They are clearly diagrammatic, and do not represent any particular sections. When describing the ontogeny, de Beer (1928, p. 163) mentions "neural folds" and Forster-Cooper in Parker & Haswell (1947, p. 52) "medullary folds." Perhaps Hatschek's figures are wrong, in that where the "fold" is moving over the medullary plate he represents one layer only of ectoderm in the "fold" instead of two. But exactly the same applies to the figures by Conklin (1932). In later stages after the delimitation of the notochord as well as the nerve cord the layers are complete. In corresponding stage of the Ascidians, *Phallusia* and *Clavellina*, there are three layers altogether, as might be expected; longitudinal sections of *Clavellina* (after Van Beneden & Julin) may be compared with Hatschek's transverse sections in Parker & Haswell (1947, v. 2, fig. 29,30,47). These neural folds and their migrations the writer regards as a fairly close ontogenetic recapitulation of the migration of two or three pairs of nerve cords towards the mid-line in the evolution of the vertebrate.

It is noteworthy that whereas in the more primitive annelids and arthropods the postcephalic central nervous system is still two separate chains forming a ladder-like structure, in even the most primitive vertebrates the two halves of the system are intimately united throughout the entire length. We may argue from this that in the vertebrate the factors causing migration were stronger.

In both articulates and vertebrates migration of the nerve cords occurred early. In the former, which lived in close relation to the floor of their water habitat, it was downward, and toward the mid-ventral line. But in the early vertebrate, which was independent of the bottom, but dependent on floating food and stimulated by light from above, migration was upward and toward the mid-dorsal line. Migration either up or down of lateral cords in the ectoderm would approximate the cords of the two sides; and, as both worms and vertebrates swim by lateral undulations, this might be expected mechanically to shift the non-muscular cords. Still another principle tending towards approximation of the cords in the mid-line is the obvious advantage in a ladder-form nervous system of close association of the two chains.

In the vertebrates the migration of the cords appears to have been very much more

rapid than in the articulates. This can be attributed to their rapid development of swimming. In the vertebrates, the stimuli of food and light would act from the first, independent of the rate of swimming. But as locomotion became more and more efficient, the migrating nerve cords would be subjected more and more intensively to the alternate contraction and expansion effected by the longitudinal muscles of the body wall involved in the locomotion; and this would tend to shift the non-muscular nerve cords of each side more rapidly, towards the animal's median plane, where both contraction and expansion die out, and only bending remains. The tendency of the nerve cords to shift directly towards the median plane culminated in enclosure of a median water space, the neural canal. The ectoderm cells lining this canal, being sealed off from the surrounding medium, have probably remained largely in their primitive condition. This is ciliated epithelium; and so suggests what was the character of part, at least, of the ectoderm at that early period, even in the prot-arthropod. There might indeed be ciliated nuchal sense organs involved in the neural folds.

Inasmuch as great changes are often the result of a conjunction of several factors, it may well be that supersession of the articulate gut by that of the vertebrate, as claimed above, was an important additional factor in the origin of the neurocoele. The former gut may have been connected by median mesenteries with the mid-dorsal and mid-ventral lines of ectoderm. If so, as the vertebrate gut superseded the arthropodan in function, the latter would probably shrink. It is argued below that the old gut has disappeared entirely, and if it shrank, it would draw down with it the ectoderm of the mid-dorsal line. In this way the formation of the neural groove, the neural folds and the neurocoele may all have been greatly facilitated.

But if the above is a fairly true picture of the origin of the spinal cord, how are we to account for the spacious cavities of the primitive vertebrate brain? To this perhaps no detailed satisfying answer can be given as yet. Because great cephalisation existed, and velocity of forward motion was rapidly attained, it would be surprising if the anterior part of the nerve cord were just like the rest. Some features of the head could not fail to exercise control over the migration of the nerve cords; for they embraced a complex and bulky brain inherited from the polychaete but subretroverted for the arthropod, a complex head made of 6 normal segments above, besides the rostrum and the labrum below, olfactory and other sense organs including two different pairs of ventral eyes, originally prostomial, a pair of "rostral," and six pairs of dorsal eyes belonging to adjacent segments. At least we can suppose that the developing head and the pre-existing sense organs still in the ectoderm would control the advance of the neural folds at the anterior end.

In the origin of the central nervous system just sketched, what originally were most dorsal in position now form the ventral plate of the spinal cord; then follow the ventro-lateral parts of the cord with the ventral nerve roots; and, finally, what were most ventral in position are now the dorso-lateral parts with the dorsal nerve roots. This great reversal explains why the dorsal roots serve the ventral side of the body and the appendages. *Amphioxus*, where the dorsal and ventral roots do not join, still exhibits a feature which finds its complete explanation in our theory. The visceral nerves arise from the dorsal roots and pass via the metapleural folds to the dorsal side of the gut. In the fishes, however, where we have the junction of the dorsal and ventral roots, this longer course is short-circuited via the ventral root.

The writer has shown how in the evolution of the polychaete the visceral nervous system had three times over been extended at the expense of the central (Raw, 1949). In the evolution of the vertebrate such a transfer from central to visceral nervous system occurred anew, and on a vast scale.

No mention has above been made of the neurenteric canal, which has puzzled many —the gut lined with "endoderm" is in that stage of development quite continuous with the neurocoele lined with ectoderm. But in the phylogenetic stage, to which that stage in the ontogeny points back, the cell layers that became the linings of these tubes were in each case bounding external space, i.e., were ectoderm. Thus on the theories here advanced the difficulty disappears.

It will perhaps be agreed that the central

nervous system and the sense organs of the vertebrate are very strongly in support of the author's theory and very strongly against the derivation of the vertebrate from the Tunicata and the Echinodermata.

11. THE NOTOCHORD

Another great and new feature, in which again the chordates are unique, is the possession of the notochord, which gives them their newer name. With the exception of Gaskell, few writers seem to have concerned themselves greatly with its mode of origin. He suggested that just as the spinal canal was, as he believed, a discarded gut, so the notochord was another, which had followed the first in use, and, in its turn had been superseded by a third, the present gut. His mode of origin of the spinal canal has been discredited above (see section 10), and his origin of the notochord must also be carefully weighed. Like the other changes above discussed, the origin of the notochord seems to be closely connected with the acquirement of free swimming. For undulatory swimming, an elastic rod in the axial plane and in the axial line should have been a manifest great advantage. As the propulsive waves passed back through the body, it should, after being bent, tend to return through zero to an equal bending the other way. The notochord is cellular, and the special turgidity of its vacuolated cells gives rigidity and elasticity, which is further increased by the strength and resiliency of its two sheaths in tension. Hence the question to be decided is how did it arise: did it arise *de novo*, or from a preexisting structure adapted to a new function, and, if the latter, which structure?

The writer agrees with Gaskell as to the secondary origin of the vertebrate gut, but he disagrees as to the origin of the neural canal. It follows therefore that on the theory here advanced the evolving vertebrate had the arthropod gut to spare. Had Gaskell himself advanced the claims made above by the present writer, he would possibly have attributed the notochord to a modification of the spare arthropod gut. And it may be noted that just as in the theory so far developed the arthropod gut directly underlay the nerve cord, so in primitive vertebrates today and in the early stages of all of them, the notochord immediately underlies the neural tube.

On the other hand, in vertebrate ontogenies the embryonic enteric cavity or "archenteron" becomes the chordate gut, and in *Amphioxus* and *Petromyzon* this "archenteron" definitely gives origin to the notochord and to coelomic pouches, after which the nerve-cord, the notochord and the gut lie in descending order with nothing between them. In higher forms, right up to man, though the presence of yolk brings modification, development leads early to the same superposition of organs, which only in later development are separated by mesodermal products.

These facts offer the following alternatives: either the notochord is a modification of the articulate gut in defiance of the biogenetic law, or it is a development of the dorsal part of the vertebrate gut, as is suggested by their ontogenies, especially all the more primitive forms. The origin of the central nervous system in the ontogeny is claimed above (section 10) as a close recapitulation of the phylogeny. The writer here again accepts the suggestion of ontogeny, and claims that the notochord is a modification of the dorsal part of what was to become the vertebrate gut. One can imagine, that, in the evolving vertebrate, the dorsal groove of the above deduced "food basket" (see section 9), already in the median plane, sufficiently coincided also with the axial line, and that its cells were already highly turgid. As nature found a new use for this turgidity, she improved upon it by pinching it off from the gut, and surrounding it with two tightly stretched sheaths which are secretions by these cells. Kerr (1919, p. 290) describes the first as "thin, elastic highly refracting and *cuticular*," and the second (inside the first) as also "*cuticular*, but thicker and more jelly-like." These descriptions suggest secretion by the ectoderm of an arthropod. Though ontogeny has been rather a "broken reed" in the past, so far as indicating the phylogeny of the vertebrate is concerned, the origin of the notochord in ontogeny is fully in support of this view. We need not suppose with Gaskell, that the evolving vertebrate has had three successive separate guts, but that it had two, of which the dorsal strip of the second became modified and divided off to form a dis-

tinct cylinder, the notochord. Its subsequent extensive change of form and its reduction by the ossicles of the vertebral column replacing it are universally accepted.

In *Amphioxus* and its relatives, which in their apparently complicated history have retained a ciliary mode of feeding for even the adult stage, the new gut, after separation of the notochord, experienced the development of another dorsal ciliated food groove throughout its pharnyx. This suggests how the notochord originated.

Indeed in the ancestor of the craniate vertebrates a second notochord did actually develop. Vertebrates, up to the grade of Amphibia, often exhibit a vestige of a second notochord, the so-called hypochord. Kerr (1919, p. 290) writes,

> "This organ (see Gibson 1910) arises after the notochord, and in an entirely similar manner. . . . On its surface it normally develops a primary sheath precisely like that of the notochord. . . . The fact that it does not occur in *Amphioxus* has rendered possible the suggestion that it represents the longitudinal groove which in this animal runs along the mid-dorsal line of the pharyngeal wall. But this idea is negatived by the fact that the hypochord extends right back to the tail, and is not merely a pharyngeal organ."

This last stricture cannot be accepted, for on the theory above developed the ancestor of *Amphioxus* had gill slits and the hyperpharnygeal groove throughout the body. The duplication of the gills in front and closure of them behind could in this case be attributed to the mode of life—almost buried upright in the sand. The hypochord can then be claimed as a second formation of notochord, and as indicating that after the formation of the true notochord a second food groove developed, while yet the posterior gills and "gill-slits" existed. Seemingly, this second food groove formed a second notochord when the posterior gills and "gill-slits" aborted.

12. INFERRED VESTIGES OF THE ARTHROPOD GUT

According to our theory the vertebrate evolved from the arthropod, but the modern vertebrate has nothing comparable with the arthropod gut. The only organ which the writer would suggest is a vestige of the arthropod gut is the hypophysis, which may be its anterior extremity. Of the rest of that alimentary canal no vestige can be indicated. Not only has it disappeared from the adult, it is not even indicated in the ontogeny. The "archenteron" resulting from gastrulation leads in the most primitive forms directly to the vertebrate gut.

Further, the lining of the gut, which in the ontogeny is traceable back to the endoderm of the embryo, has in the phylogeny been derived from the ventral exterior, i.e., the surface of the body and appendages, of the prot-arthropod. Ectoderm of the ancestor is represented by endoderm of the modern embryo!

One can imagine that after the complex evolution of the vertebrate the ontogeny also was at first correspondingly complex, representing the development first of articulate and then of vertebrate; but in time the features of the first were more and more curtailed until they disappeared altogether (principle VI).

The pituitary body may be a case of old digestive glands of the articulate taking on in the vertebrate a new function.

13. REDUCTION OF THE GILLS AND CHANGE IN THE MYOTOMES

As the efficiency of the gills for respiration was increased, both by their own development and by habitual and rapid swimming, they were no longer needed on all the segments present in the ancestor, and they ceased to be developed on any but the anterior ones. Further, to judge by fossil and recent forms, they were relatively early reduced in the gnathostomes to about ten. This curtailment originated the difference between the pharynx and the rest of the gut.

More immediately connected with the development of swimming speed, indeed responsible for it, were the extensive changes in the musculature, namely, the suppression of the circular muscle layer if such persisted, and the special development of the longitudinal muscles within each segment, till they practically filled them, and formed the myotomes. Further increasing the efficiency of the latter for locomotion was the change in their form—from plane transverse, to the sharp angulation seen in *Amphioxus*, and still further, to the triple angulation seen in

the higher fishes. This would help to promote perfect continuity in the undulations.

14. THE VERTEBRATE BODY CAVITY

Another new development, that of the splanchnocoel (the ventral continuous body-cavity), is perhaps difficult to envisage. The advantage to the fish of the independence of the gut from the muscular body-wall is obvious. In some way, when the continuous new body-wall formed on each side of the new post-pharyngeal gut, the appendicular branches of the coelomic pouches also joined up into a continuous splanchnic coelom, over which later the myotomes extended as undulatory locomotion was perfected.

In the ontogeny of *Amphioxus* this phylogenetic change is beautifully repeated, for the splanchnocoel is at first segmented, and later "the partitions between the splanchnocoelic sections of successive somites break down, so that the splanchnocoel becomes a continuous cavity from end to end of the gut" (Bourne, 1902, p. 199). The origin of the body cavity can be regarded as a natural result of the undulatory swimming of the fish. It allows the gut to have less undulatory motion than the body walls.

15. EVOLUTION OF THE FISH FORM

Characteristic of the typical fish is the laterally compressed body, adapted to undulatory propulsion, combined with a streamlined spindle form to facilitate the locomotion. As Dean expressed it, "aquatic life has stamped them in a common mould, and has prescribed the laws which direct and limit their evolution." This body-form is a primitive chordate development, and had been already evolved in the earliest free-swimming fishes known—the Anaspida, and at least behind the head, in the Pteraspida. Its evolution would accompany the other changes.

A thin strip that can be thrown into rapidly moving waves travelling along it (from front to rear for forward movement) is essential for this kind of locomotion. However, propulsive muscles are voluminous, located in space that is needed also by other body organs. An accessory factor favouring speed is the presence of numerous mucous-secreting cells in the skin, the secretion of which evens up the surface and reduces friction. Richardson (1936), however, could not see evidence of this.

The early arthropod from which the fish had evolved may have had a widely different form, as befits an adult benthonic life. It was long, depressed, and with lateral compound appendages on every normal segment, each comprising a pleuron, walking leg, and gill.

In the foregoing discussion of vertebrate evolution much has been said about the gills and their reduction in number, but nothing about their form. Primitively these must have been external and probably pinnate as in the arthropod but now except in the larvae of a few freshwater forms and in the larvae of Amphibia they are internal, sessile and lamellar. Kerr (1905–6, 1907) expressed the view that the external gills were organs of great antiquity and had preceded the internal gills, and also that the respiratory epithelium lining the existing gill clefts and constituting the gills had spread inwards from the external gills.

For the locomotion of the fish it was certainly of advantage to dispense with the resistance offered by the external gills, and Kerr's suggestions indicate how it could be effected. Presumably, for a long time the change took place in the ontogeny, the larvae having external and the adults internal gills, as still occurs in the primitive fishes above mentioned. By this view the external gills can be regarded as handed down not only from the early vertebrates, as Kerr believed, but even from the ancestral arthropods. This change from external to internal gills together with the closure of all the gill "clefts" not needed would greatly help to stream-line the body surface and so favour speed.

At the same time and to the same purpose the body was greatly shortened, so that for the most part, when swimming, it is not longer than a complete body-wave comprising a right and a left out-bowing. There are however "exceptions to every rule": for example, the eel has a long body which when swimming exhibits more than a complete wave, indeed two waves according to Marey. In view of its ontogeny, however, this can be regarded as a secondary adaptation to its adult mode of life.

Like other animals, fishes survive in the struggle for existence in different ways, by speed, armour, invisibility, or concealment. When one considers their ancestry and their habitat, the test of real progress may be taken to be speed. For this, four factors are pre-eminent: (1) body form, (2) efficient muscular and nervous systems, (3) flexible and thin armour, and (4) lubrication. In each of these features the fishes are supreme among swimming animals.

There are however among fishes so many ways of making a living, that the most specialised are far from being the fastest swimmers.

16. THE COMPOUND DEPLOYMENT INTO THE MONORHINAL AGNATHA AND THE DIPLORHINAL GNATHOSTOMATA

Important divergences must have appeared very early in vertebrate ancestry for the early Palaeozoic chordates can be divided into two subphyla, the monorhinal Agnatha and the diplorhinal Gnathostomata.

Of the two divergences one would think that the division by the olfactory orifices being a median single one, or a symmetrical pair would come first, to be followed by the reduction of the appendages in the Agnatha or the use of them for jaws and limbs in the Gnathostomata.

The latter as they evolved would appear to have ingested larger and larger food and some of them, as their powers grew, fed on more and more formidable prey.

In the Gnathostomata an anterior pair of appendages, owing to their position, came to function as jaws for seizing all sizeable food; and owing to their attitude the distal halves of these right and left appendages acting together became the lower jaw, and the proximal halves became the upper jaw.

It is not necessary to suppose that primitively it was the same pair in all branches. There may have been divergences of which we know nothing as yet. The labial cartilages may represent an anterior pair of limbs immediately in front of the mandibular, which were superseded because of their weakness. Kerr regarded them as "of no important morphological significance"; but on the contrary most vestiges are keys to morphological problems. The later association of the mandibular arch with the cranium, and the support furnished by the hyoid arch in later times, are generally recognised.

Exactly which segmental pair it was that became the jaws of modern vertebrates may be in doubt, but it is deduced (section 5) to have been the third in front of the occipital segment of the arthropod. Gaskell believed that they belonged to the occipital segment i.e., that which in the writer's view corresponds to the 6th segment behind the peristome of the ancestral polychaete; and he believed that the thyroid gland belonged to the next segment but one behind.

Many have thought that the Agnatha gave rise to the Gnathostomata, but as the Agnatha are monorhinal this is extremely improbable.

17. THE MEDIAN FIN—A VERTEBRATE DEVELOPMENT

It is important to determine, if possible, what was the primitive condition, and also what was the primitive function of the various fins, for functions change readily in adaptation to new conditions.

The median fin, comprising dorsal, caudal and ventral (or anal) has been regarded: (1) as constituting a unit; (2) as being older than the paired fins (e.g., Dean, 1895, p. 31; Jordan, 1905, p. 63; Young, 1950, p. 79); or (3) as being of the same nature as, and a continuation of, the paired. All of these views are here opposed.

(1) Is the median fin a unit? No. In *Amphioxus* the dorsal and the ventral are distinct. The fin rays supporting the dorsal are single, whereas those supporting the ventral are paired. This ventral fin also extends forward to the atriopore, beyond which are the paired metapleural folds. These conditions suggest that the ventral fin has a quite different origin from the dorsal, that it is due to a coalescence in the mid-line of the pairs of pleura of the posterior segments so as to extend the undulating surface for swimming, and that in front of the atriopore on each side the pleura have coalesced into a lateral fold, and extended down over the pharynx, while branches unite with those of the other side in the mid-line serving thus as a protection against the sand for this part, in adaptation to its burrowing habit. The median fin behind may well indicate the origin of the ventral me-

dian fin (often called the anal) of fishes in general. On this view the dorsal fin has a quite different origin from the ventral or anal. It could not form till after the closure of the neurocoel. This is perhaps a new theory (compare Whitehouse, 1918, p. 137). It derives support also from the fact that in elasmobranch development the dorsal fin commences with distinct segmental muscle buds from the pairs of myotomes, but "In the anal fin and the caudal fin distinct muscle buds do not occur, the radial muscles being derived from proliferations of cells from the ventral border of the myotomes" (Goodrich, 1930, p. 115).

(2) Is the median older than the paired fin? No. If one accepted the latest edition of the popular theory, namely, derivation from near the echinoderm through the tunicate, which on that theory are primitive, not degenerate, and by neoteny have given rise to the chordates (Young, 1950, p. 49, 72–77; Berrill, 1955), we could conclude that the median fin was the more primitive. But if, as I believe, the paired fins represent arthropod pleura derived in turn from foliate lobes of the polychaete, they have a colossal antiquity. On the other hand the dorsal fin is not, as is the paired, an inheritance from the articulate; instead it is a vertebrate development, as is indicated by the existence of the neural canal, and its necessary mode of origin. It is a skin fold, which developed early, and still is present in tunicates, *Amphioxus*, and fish. Both in Elasmobranchs and in higher forms it is furnished with skeleton and with muscles extending into it from the myotomes. Its function is to increase the surface effecting propulsion and turning, to actively share in these functions, and also to serve as a vertical keel. The development of a dorsal and ventral fin to the end of the body resulted in a diphycercal tail found still in many fishes and especially in fish larvae. This suggests that this form was developed early in chordates—protocercal.

(3) Are the median and paired fins of one and the same origin? No. In answering 1 and 2 we have at the same time answered 3 in detail. Norman (1947, p. 56) expressed the view that the paired fins are a split continuation of the median through the anal fin. He thus implies that all the fins constitute a unit. Goodrich (1930, p. 124) also stated, "An examination of the development of the paired fin shows that in every important particular it resembles that of the median fins." On the contrary, as he himself points out, in our most primitive gnathostomes, the Elasmobranchii, the paired fins have two muscle buds per segment, whereas the dorsal fins have only one. This, one thinks, must be significant.

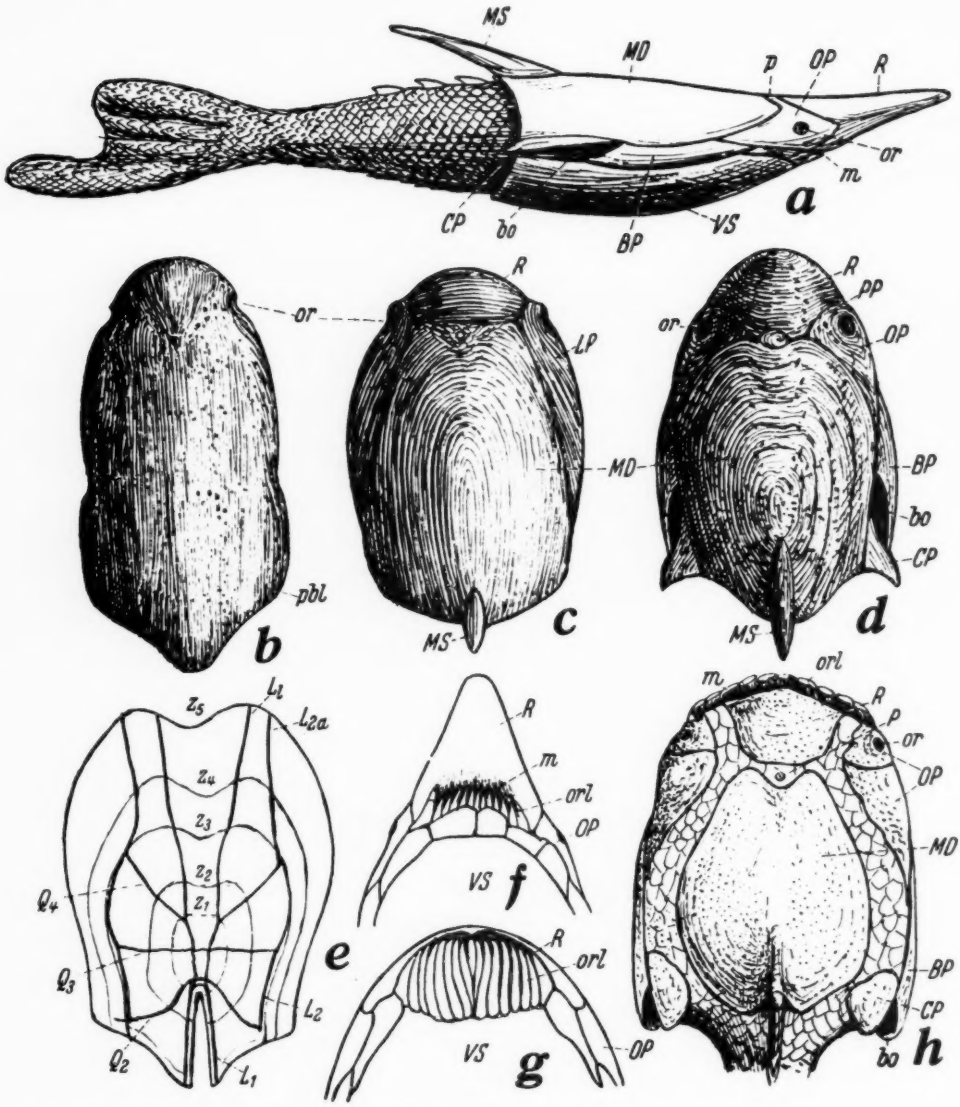
As expressed above, the dorsal part of the median fin must postdate the development of the vertebrate spinal cord, and the ventral part must likewise postdate the development of the alimentary canal and ventral body-wall, so that the whole median fin is obviously a vertebrate development.

18. HETEROCERCAL AND HYPOCERCAL TAILS OF EARLY FISHES

The earliest well-preserved fossil "fishes" are Agnatha and related, it is believed, to modern cyclostomes. If so, they would not have an air-bladder, and so would be heavier than the water, especially as this was fresh. Those that were strongly armoured were especially heavy. The most primitive are of two contrasted types: the primitive Osteostraci (Cephalaspida, text-fig. 3*a–j*, and Anaspida, text-fig. 4*a* and *b*) and the less primitive Heterostraci (Pteraspida, text-fig. 5,6). All are very different from any modern form and extremely different also from one another, indicating how very early was the origin of the chordate.

The CEPHALASPIDA are in several ways the most primitive of craniates. Between the head and tail, where it is difficult to count segments, there are more than 60 similar segments each defined by its own large scales, and each with its pair of lateral fins (ventro-lateral and latero-ventral scales) closely comparable with the pleura of primitive arthropods. The cross-section throughout this part of the body is an elevated triangle adapted for resting on the bottom, with the ventro-lateral and latero-ventral "scales" (fins) extending from the bottom corners to provide further support. The dorsal fin except for dorsal scutes is limited to one or two triangular fins (see Stensiö, 1927, 1932; Heintz, 1939a).

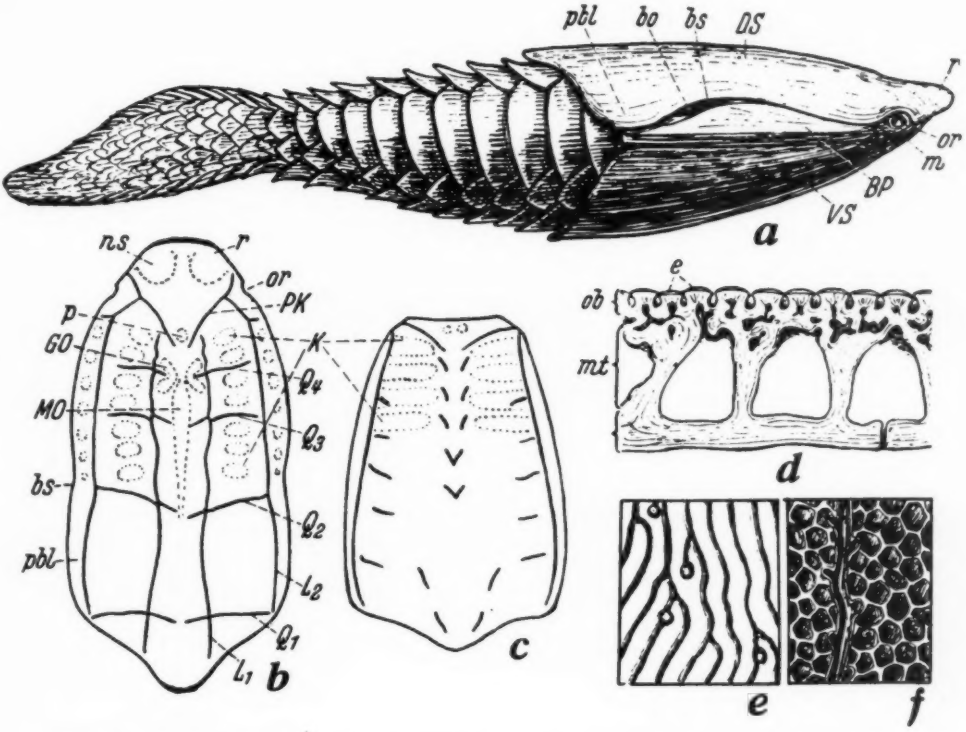
In front of these normal segments is the large roughly semicircular head, arched



TEXT-FIG. 5. Heterostraci. All from A. Heintz, 1938, p. 52, fig. 2.

a, Restoration of *Pteraspis rostrata* (after White). *b*, *Poraspis*, dorsal shield (after Kiaer). *c*, *Cyathaspis*, dorsal aspect of head shield. *d*, *Pteraspis*, dorsal aspect of shield with sense lines; *e*, median dorsal plate of *Pteraspis* with sense lines and growth stages (after White); *f*, arrangement of plates around the mouth in *Pteraspis* (after White). *g*, The same in *Pteraspis vogti* (after Kiaer). *h*, *Drepanaspis*, head from above (partly after Patten).

Features on figures: bo, branchial orifice; BP, branchial plate; CP, cornual plate; L1, L2, longitudinal sense-canals; LP, lateral plates; m, mouth; MD, mediodorsal plate; MS, median spine; OP, orbital plate; or, orbit; orl, oral plates; p, pineal eye; PP, pineal plate; Q2–Q4, transverse sense-canals; R, rostral plate; VS, ventral shield; Z1–Z5, growth stages of median-dorsal plate.



TEXT-FIG. 6—Heterostraci. *Poraspis* from Spitzbergen (after Kiaer & Heintz, 1935). All figures from Heintz, 1938, p. 50, fig. 1.

a, Restoration of *Poraspis* in side view; *b*, dorsal shield without sculpture, but with the courses of sense-canals in black line and the impressions of the organs on its ventral side in dotted line; *c*, ventral shield with courses of sense canals (black) and with gill pouches of its inner side (dotted); *d*, cross-section of a shield greatly magnified (no trace of bone cells to be seen); *e*, surface of head shield, magnified, showing the dentine ribs and the pores; *f*, part of shield from which the surface is removed, magnified, showing the cancellous layer traversed by a sense canal.

Features on figures: b, basal layer; bs, branchial sinus; bo, branchial orifice; BP, branchial plate; DS, dorsal shield; e (in D), dentine ribs; GO, impressions of semicircular canals; K, impressions of gill sacs; L1, L2, inner and outer longitudinal sense-lines; m, mouth; MO, impression of medulla oblongata; mt, middle spongy layer of shield; ns, impressions of nasal sacs; ob, upper layer of shield (dentine); p, impression of the pineal organ; pbl, post-branchial lobe; PK, pineal sense-line; Q1–Q4, transverse sense-lines; r, rostral part of shield; VS, ventral shield.

above, but flat below, where the mouth and the gill openings of each side are arranged in a circle. Within the posterior corners of the head some forms have a pair of pectoral fins, which are best interpreted as a development of the coalesced pleura of the immediately succeeding body segments. But these Osteostraci exhibit various stages of cephalisation, and some, instead of bearing these fins have a number of the body segments coalesced with the primitive head. Moreover, behind the normal segments and the anus, they bear (at least in *Hemicyclaspis*) a pair of horizontal fins, as discovered by Stensiö and interpreted by Heintz (1939a), followed by a heterocercal tail, the axial lobe being bent upward and bearing its fin mainly below. That they are quite off the line leading to modern fish is indicated by their armoured cephalon, their retention of pleura on all normal segments, and their post-anal horizontal pair of fins. Their build—heavy head, triangular section, ventro-lateral scales, post-anal paired fins and

heterocercal tail—all suggest a benthonic mode of life. As to the primal function of the heterocercal tail, Harris (1936) claimed that in the dog-fish such a tail is necessitated by the activity of the pectoral fins in lifting the head, the function of the tail being to compensate for this by giving a lift to the rear. But pectoral fins could act equally well to give lift or drop. All *early* fishes took their rest on the bottom, and in the writer's view the primitive function of the uptilt of the tail was to apply itself to water rather than to mud, and it contrasts with the function of the hypocercal tail of the anaspid.

The ANASPIDA (text-fig. 4*a*,*b*), first extensively revealed by Kiaer (1924), are a great contrast. Their very light exoskeleton, numerous segments giving great flexibility, and vertically extended triangular section suggest that they were excellent swimmers. Their surviving gills are indicated by a row of round apertures descending posteriorly behind the head; there are 6 in *Lasanius* (Bulman, 1930), 8 in *Birkenia* (Traquair, 1898) and *Rhyncholepis*, 10 in *Pterolepis*, and 15 in *Pharyngolepis* (Kiaer, 1924). Pectoral fins are represented by a pair of spines projecting laterally from a segmental exoskeletal element and situated a few segments behind the last gill aperture (Kiaer, 1924, p. 79,81), or there may be a segmental succession of these (*Lasanius*, Bulman, 1930). In these genera the only function of these spines would appear to be support on the bed of lake or river, but in one genus at least, and perhaps two, paired fins are well developed (Stensiö, 1939). In *Endiolepis*, an Upper Devonian form, an extensive row of conspicuous segmental ventro-lateral scales, united at their edges, extend out at right angles to the body, closely comparable with arthropod pleura. They adjoin a row of shorter scales forming the ventral edges of the sides of the abdomen up to the anus, behind which is a triangular anal fin. *Endiolepis* also has a dorsal fin, although most other Anaspida have dorsal fins represented only by spiny scutes.

All Anaspida have a hypocercal tail, the axis having a marked downward bend and with the tail fin limited to the dorsal side of it. This type of tail, the opposite of the heterocercal, has perhaps not hitherto been interpreted. To the writer it signifies the opposite mode of life from the benthonic. The Anaspida, great swimmers as their body form suggests, probably got their food mainly from the water surface. Primitively they turned down their tail to cause it to apply itself to water rather than to air, further inclining the body, head up toward the surface.

The PTERASPIDA (text-fig. 5 and 6), the third ostracoderm order mentioned, are again very different. They agree with the last in that their tails are hypocercal and that the post-cephalic parts of the body are well built for swimming; but the cephalic and greater part of the body is encased in armour between great dorsal and ventral shields. The gills were served by the mouth in front and a single lateral posterior opening on either side halfway up the profile. This kind of fish was well designed for resting on the bottom as well as for swimming. The streamlined posterior part of its body and its hypocercal tail suggest that, before it secondarily adopted a largely benthonic life, this fish was a good swimmer. However, the hypocercal character of its tail is not as pronounced as in Anaspida, and may be a response to the weight of the anterior armour.

The general presence of heterocercal tails in the early fishes suggests that they are derived from somewhat benthonic ancestors. One can imagine that when they reached lakes, where the current was negligible, many vertebrates, in the absence at that stage of swimming bladders, subsided to the lake floor and made it their usual abode as well as places of repose.

Romer (1933) suggested that the armour of the early fishes was a protection against the predaceous eurypterids, both groups inhabiting the same waters at the same time. This seems possible as regards the armour of both early Agnatha and fishes. In Precambrian time the ancestors of both chordate and chelicerate had ascended the rivers, and they were in this antagonistic relationship in the upland lakes of the North Atlantic continent. The origin and ascent of the vertebrate are claimed in this, and those of the chelicerate in a previous paper (1957).

But H. W. Smith (1943) as pointed out by Berrill (1955, p. 235) offers an alternative explanation of the accumulation of

bone in so many of the earliest fishes, namely, that it was due to the change of habitat from salt sea water, to which their ancestors were necessarily adapted, to the fresh waters of rivers and lakes. Smith believed that "the ever-present armour of the fossilised vertebrates of Silurian and Devonian time was a defence against the osmotic invasion of fresh water rather than the claws and tailspines of Eurypterids." To Berrill (1955, p. 236–242) this is "closer to the truth," but he adds an excellent discussion on the skeleton of vertebrates in his last chapter, pointing out that the excretory system in the change to fresh water had to deal not only with water but with an abundance of calcium carbonate and phosphate, and the skeleton was over developed "because of inability to eliminate the salts fast enough by any other means." They "became bottom feeders because they were too heavy to be anything else." One might add that an important factor in their inability to adapt themselves might be the fact that the change was so abrupt from marine to fresh waters. But one must keep in mind that there were also the Anaspida.

19. THE PAIRED FINS

Except for Kerr, there has been striking uniformity of opinion among later zoologists as to the origin and significance of the paired fins. They are regarded as specially developed parts of continuous fin-folds evolved in the chordate, and this view is repeated in the latest text books. Many indeed have believed that they are of the same nature as, and indeed a bifid continuation of, the median fin as already stated (Woodward, 1892; Norman, 1935, 1947).

Kerr (1919, p. 443–453) discussed the two theories most widely held up to that time—the "Gill-septum Hypothesis" of Gegenbaur (1872) and the "Lateral-fold Hypothesis" of Balfour (1878). He gave reasons for discarding both those theories, and from his studies of primitive fishes he advanced in their place the theory he had previously proposed (Kerr, 1907, p. 274–5), viz., that the paired fins are derived from external gills. These were known to occur in *Polypterus* then included in the Crossopterygii (and which later Goodrich claimed as a Palaeoniscid), in two of the three known Dipnoi (*Lepidosiren* and *Protopterus*) and in Amphibia; apparently no other typical occurrence has since been discovered. Kerr concluded that external gills are "organs of high antiquity in the vertebrate stem"; that "an external gill was once present on each visceral arch"; that these originally "extended tailwards beyond the limit reached by the branchial region of existing vertebrates"; further that being also "potential organs of support" and "potential organs of movement", "they possess the qualifications . . . for the evolutionary forerunner of the vertebrate limb." Later (1921, p. 391) he suggested that two single pairs of external gills had given rise to the pectoral and pelvic fins.

This is an interesting theory. The writer accepts the early statements quoted, for on his view external gills characterised all the normal segments of the primitive arthropod, and were inherited by the evolving vertebrate, but he believes that the paired fins had quite a different origin.

The theory here put forward proposes that the paired fins were directly inherited from the pleura of the prot-arthropod, which in turn had inherited them from foliate lobes of the notopodium of the polychaete. The evidence for the lateral "finfold," a pure invention, equally supports derivation from the continuous row of appendages of worms and arthropods. Few who carefully compare the paired fins of the earliest fishes, the elasmobranchs (e.g., *Cladoselache*) and placoderms (Acanthodii), the ventro-lateral "scales" of cephalaspids and the anaspid *Endiolepis* (Stensiö 1939), the pectoral and succeeding spines of *Lasanius* and other Anaspida, the pleura of trilobites and the paddles of the polychaete will doubt their homology. Such structures extend no farther rearward than the anus, for the forward shift of position of the anus was connected with a change of function of the posterior part of the body. Special functions in locomotion led to the replacement of appendages and the gaps between them by the even surface of the tail. In the "fish" the pleura migrated ventrally, as is indicated by the oblique line of the gill apertures in Anaspida. Behind the anus the pleura of the two sides have coalesced in the mid-ventral line, so as to form the ventral part of the

median fin. Only one group seems to differ: immediately behind the anus, the Cephalaspida have an extensive horizontal fin on either side of the caudal fin. It is covered with small scales, and seems to be a direct continuation rearward of the line of the ventro-lateral scales, as Heintz states (1939, p. 68). Therefore, by our theory each is an association of post-anal pleura. If this is a correct interpretation it supports the conclusion, suggested by other facts, that the Osteostraci diverged very early from a progressive line of vertebrates. Behind these lateral post-anal fins the ventral fin of the heterocercal tail is a coalescence of pleura.

Hence the paired fins of fishes were not developed from parts of a continuous finfold, but from groups of a continuous succession of originally separate segmental pleura, parts of segmental appendages, which, in the prot-arthropod, as in early trilobites (Olenellidae, Paradoxidae, and many others), were still moved by muscles, and which in the ancestral polychaete (as in modern Phyllodocidae) by rhythmically beating the water, were useful in locomotion. Indeed, in the ancestry of the Osteostraci, Elasmobranchii and of all the higher fishes there is no reason to believe that they ever ceased to be moved by muscles or to be useful in locomotion or balancing. This view is in marked contrast with all others, e.g., with that of Young (1950, p. 30) and that of Heintz and others, discussed below.

Within fishes, using the term in the widest sense, we find extremely varied development of the "pleura." In cephalaspids, which probably separated from the anaspid stock very early, each normal segment bears a pair. They are relatively unmodified, and form ventro-lateral supports when resting on the bottom, and probably paddles when swimming, with the exceptions above mentioned. The same appears to be the case in the anaspid *Endiolepis* (Stensiö, 1939). In other Anaspida they are extensively suppressed, but a relatively anterior pair is represented by the pectoral spines, which are followed in some forms by a series of progressively diminishing spines. In the Cyclostomata (Petromyzontia and Myxinoidea) they are entirely suppressed.

In the placoderm Acanthodii we have a condition which suggests that in its many segmented ancestors there were periodic specialisations of groups of pleura into periodic pairs of fins. What might well determine the number of these pairs of fins would be the number of half-wave lengths in the undulatory motion of the fish. All but the most anterior and most posterior pairs were undergoing suppression, which suggests that this periodic specialisation preceded a great shortening of the body to a single wave length, when all but the pectoral and pelvic fins had become degenerate. The fact that these degenerate pairs occur only in the Acanthodii might be due to the persistence of the massive spines associated with the fins in this order. This view is supported by the fact that no fin web is associated with the intermediate spines.

This consideration suggests that the unknown early vertebrates were proportionately very long bodied; above it has already been claimed (section 7) that they had great numbers of segments. In the Elasmobranchii and in the bony fishes only the pectoral and pelvic paired fins appear in known forms, and these are possibly, indeed probably, as suggested by the Acanthodii, the foremost and hindmost members of a series, of which only these survive owing to shortening of the body in the acquirement of the optimum proportionate length.

Goodrich (1930, p. 131, fig. 143) describes and figures the segmentation in a 19 mm. embryo of the dogfish, and the innervation of the lateral and dorsal fins in the adult. In the embryo the muscle buds are much more numerous than in the adult suggesting the primitive condition when they were developed throughout the body. By our theory the dorsal fins are vertebrate extensions of the segments, whereas the paired fins are inherited annelidan extensions. In the adult, according to Goodrich, the pectoral fin is innervated by the spinal nerves numbered 1 to 13 and the pelvic by nos. 25 to 35, whereas the 1st dorsal is served by nos. 25 and 43 and the 2nd dorsal by nos. 44 to 57. Each paired fin on our theory is a coalescence and concentration of the pleura of the numbers of segments indicated, respectively 13 and 11. In the 19 mm. embryo, however, concentration has begun in the pectoral but not in the pelvic; in the dorsal fins too, concentration has hardly begun; but in the adult a quite

surprising concentration of the muscle buds and nerves is indicated. The concentrations are all related to the evolution of swimming efficiency as discussed in part by Harris. The shortened bases of the paired fins allow of rotation towards transverse positions.

The functions of the paired fins have probably always been complex. In the elasmobranchs, heavier than water, the pectorals act as vol-planes opposing gravity and lifting, or depressing the fish, while body and tail effect propulsion, the tail also effecting lift of this part. The pectorals also function as brakes in stopping and in turning. In the Actinopterygii in very slow swimming the pectorals act as paddles. With the pelvics they act as brakes; and according to Harris it is in connection with this function that the pelvics have, in more advanced forms, migrated to the front. On the other hand, in rapid swimming both pairs of paired fins are held close to the body so as not to reduce speed by friction and eddies. In teleosts, of about the same density as water, the most important function of the pectorals is to maintain balance necessitated by the low position of the air bladder and the high position of the backbone. In the deployment of the fishes the function of the fins has changed enormously, but it is too big a question to be dealt with here. It has been investigated by Breder, Gray, Harris and others.

20. PECTORAL AND PELVIC GIRDLES

The paired fins articulate with the pectoral and pelvic girdles, and the pectoral girdles are, in some primitive fishes, so comparable in form and position with the skeletons of the branchial arches, as to suggest that they are serially homologous with them, e.g., in *Pleuracanthus sessilis* Jordan (Moy-Thomas & White, 1939, fig. 3) or *Pleuracanthus decheni* (Goldf.). This was noted by Gegenbaur, who also believed that the girdle was a branchial arch. It is, nevertheless, much more substantial than a branchial arch, which reminds one of the contrast between the jaws and the normal gill arches. But if we study what appears to be the most primitive known example of a pectoral fin, that of *Cladoselache*, it gives the impression that the supporting cartilages are a coalescence of several separate, originally parallel bars. Hence the conclusion follows that not only does the fin represent several pleura, but the girdle, likewise, represents a coalescence of several appendages that are now represented by branchial arches.

In the case of the pelvic girdle, the presumably greater degeneration which has taken place prevents us from making close comparisons with the gill arches. One can scarcely question the serial homology between the pectoral and the pelvic girdles. It follows, therefore, on the view here advanced, that a number of the complex appendages of the prot-arthropod, and therefore also of the ancestral polychaete, constituted the prototype of each limb of the vertebrate. Furthermore, these limbs point back to the time when the gill arches and pleura extended all the way between mouth and anus, and indeed at first all the way to the posterior end of the body.

It should be noted too, that by this theory in which the appendages preceded the evolution of myotomes there is no difficulty in correlating gill arches and limb girdles (Goodrich, 1930, p. 129).

21. VASCULAR SYSTEM OF THE VERTEBRATE

The vascular systems of the annelid and of the vertebrate are often contrasted (Young, 1950, p. 47). The polychaete has typically a main vessel dorsal to the gut, in which the blood moves forward, and a main vessel ventral to it, in which it moves rearward. By contrast, even the most primitive chordate, *Amphioxus*, has the dorsal or vessels, in which the blood moves rearward, and the main ventral vessel in which it moves forward. *Apparently*, the circulation in *Amphioxus* moves the opposite of that in the annelid. This fact supports the claim for reversal of surfaces. But since by Gaskell's and by the present theory the vertebrate gut is an entirely new one, quite different from that of the annelid ancestor, and since by our theory the ancestral annelid gut has entirely disappeared from the vertebrate leaving hardly a trace behind, the circulations in the two are not immediately comparable. In the writer's opinion, the main dorsal vessel of the polychaete is not represented in the vertebrate and the main ven-

tral vessel which one might expect to occur between nerve cord and notochord is also absent *there*.

It should, however, be noted that in the pharynx of *Amphioxus*, where there are gill slits and where, therefore, it is more primitive than posteriorly where these are absent, the dorsal aorta is double, and probably was originally double for the whole length. Though now this aorta is below the level of the notochord and, except in *Amphioxus*, is a single vessel, it seems probable that originally there were a pair of vessels lying at the sides of the notochord, somewhat as in *Amphioxus* where the pair lie on either side of the hyperbranchial groove of the pharynx. It is therefore suggested that they have shifted down somewhat, and have become united into or reduced to a single vessel. Hence on our theory the dorsal aorta of the vertebrate represents the ventral vessel of the worm, which likewise was double, the two being separated by a median mesentery. The positions of these vessels are comparable, and in them the direction of the circulation is the same. Below the gut in the vertebrate the *longitudinal* system is obviously by our theory quite new, for in the ancestor this part of the body was represented only by separate pairs of appendages.

22. FRESHWATER ORIGIN OF VERTEBRATES AND ITS WIDESPREAD CONSEQUENCES

Incidentally a part of this subject has already been discussed above under The Heterocercal and Hypocercal Tails of Early Fishes.

It has often been supposed that the Vertebrata must have arisen in the ocean (Young, 1950, and many others). But that they arose in fresh water is indicated by many facts. Berrill (1955) agrees with the present author in this. Had the early vertebrates been marine, they could hardly fail to appear abundantly in Cambrian, Ordovician and Silurian marine deposits, which contain representations of the marine life of those periods, for in the Lower and Middle Ordovician there were "fish" with good skeletal parts (Miller and others, 1947; Bryant, 1936). They are fragmentary, and are here interpreted as freshwater forms transported into marine deposits. But we know very little of the fishes till towards the closing stage of the Silurian; and it is in the fresh water deposits of the Old Red Sandstone, not the marine Devonian, that they first appear in strength. The fossil record of the early fishes is almost limited to what we might call the North Atlantic continent or "Laurentia," the early fossils coming as they do from the countries on both sides of the North Atlantic. From their size, organisation, and their great variety, it is evident that they had already had a very long history; for by the Middle Devonian, all the Palaeozoic subclasses of fishes, no less than 13 in number, and amphibia also had appeared. That different classes had been evolved in different regions is suggested by the successive appearance of new types, the origin of which we cannot trace. Perhaps they came in successive invasions. The Elasmobranchii are not known before the Upper Devonian.

On this freshwater origin, in the writer's view, very much has depended.[1] As above claimed, it led to the continuous evolution of swimming capacity until lakes were reached, and there it conditioned the evolution of the heterocercal tail. Later, when the climate became arid it determined the evolution of the lungs, and through them later the successive conquest by the vertebrates of the land and of the lower air. The same change of climate towards aridity may be held responsible, as the writer believes, for the retention of external gills in the forms already mentioned. The yearly changes to marsh or drought would determine the evolution of the Dipnoi; and the fouling of the water due to those conditions may have favoured the retention of external gills.

Besides being of supreme importance for the evolution of the higher vertebrates, the evolution of lungs was also of immense importance for the fishes themselves. It enabled them to be of the same density as the medium in which they lived. The still further evolution of the lung into an air bladder within the Actinopterygii has given these the freedom of the various depths of the sea as well as of fresh waters, has caused the pectoral fins to acquire a new function as

[1] The vertebrate kidney has been referred to it (Young, 1950, p. 79–80).

balancers, and has led to vast deployment within the class. The evolution of the swim-bladder was succeeded by the evolution of the homocercal tail. Fish, which had previously lain on the bottom when resting, possessed heterocercal tails. But thanks to the new freedom a much more efficient tail for simple forward propulsion and turning was gradually acquired; and all stages in its evolution are visible in fossils. Further, it is still represented in the ontogenies of many fishes. Kerr (1921; 1926) gives the best account known to the writer of the development and evolution of the lungs and air-bladder.

Since this was written the paper by Romer & Grove on the Environment of the Early Verbebrates has been noted. Their conclusions (1935, p. 851–4) are as follows: The fishes arose in fresh water. The ostracoderms remained in this to the end of their history, for the exception that they mention (*Phyllolepis*, p. 851) should have been placed in the arthrodires. The Acanthodii and the other placoderms also remained there, except certain arthrodires and ptychodonts which migrated to the sea in the Devonian, as also did the Chondrichthyes. The Crossopterygii and Dipnoi have stayed in fresh waters but *Dipterus* is said to have become adapted to marine life in the Upper Devonian. (But of this perhaps we should remain in doubt.)

The Actinopterygii appearing in the Upper Devonian are poorly represented, but were destined to dominate in the Mesozoic seas.

23. SIGNIFICANCE OF *Amphioxus* AND THE OTHER LOWER CHORDATES

Of the other Chordata only the Cephalochorda (*Amphioxus*, etc.) are closely comparable with the true higher vertebrates. But the tunicates have by so many been regarded as our ancestors, that their status on our theory should be considered.

The most primitive chordates such as *Amphioxus* and the other sub-chordates are kept primitive through early degeneration. This is directly opposed to recent expressions of opinion (Young, 1950, p. 24,47,72, 78; Berrill, 1955). The position of *Amphioxus* in the present theory will be obvious. It presents a combination of primitive and degenerate characters. Not only is it degenerate in the adult mode of life, but its extreme asymmetry in larval stages points, according to most later writers, to a degenerate stage in its ancestry, when the adult lay on one side, instead of continuing nectonic. It is degenerate in other ways. It retains several features of a very early stage of vertebrate evolution, those already mentioned (sections 5, 6) and others including segmental gonads, nephridia and dorsal nerves, the latter derived direct from sensory cells as given by de Beer (1947, p. 18). But among the primitive features mentioned by him the absence of special head, brain and paired limbs should not be included, because in all these features it is degenerate. *Amphioxus* lost the parts mentioned at the same time that, owing to its burrowing habits, it extended its notochord to the anterior tip of the head, and coalesced its pleura into metapleural folds. Young (1950, p. 78), as did Haldane & Huxley (1927, fig. 81a,b), included, as novelties introduced in the Chordata after the *Amphioxus* stage, the head, brain and sense organs as well as paired fins. Berrill on the contrary regarded the lack of brain and sense organs as the result of degeneration.

Of special significance is the close resemblance of the nephridia of *Amphioxus* to those of the polychaete *Phyllodoce parretti* (Goodrich, 1902, 1909). This resemblance very strongly supports the theory here presented but strongly opposes the current view. According to Young (1950, p. 47), *Amphioxus* presents us with "the full plan of chordate structure as it may have existed in Palaeozoic time." But its nephridia he regards (p. 35) "one of the most mysterious features of the organisation of *Amphioxus* [because it] does not conform to the basic chordate plan, nor to their invertebrate allies, Echinoderms, Brachiopods and Polyzoa." It is indeed very strongly against his whole theory of vertebrate origins; and the same applies to the theory of Berrill.

Since *Amphioxus* still possesses annelid nephridia, it must have inherited them from the polychaete through the prot-arthropod, and its ancestor must have diverged from the progressive vertebrate line very early, even before the annelid excretory organs had been replaced and before vertebrate excre-

tory organs evolved. The divergence of *Amphioxus* was probably induced by its return to the sea, where competition was such that it could only survive by hiding.

The fact that the segmental nephridia open into the atrium, and the separate anterior "Hatschek's nephridium," similar to and homologous with the others, opens into the pharynx just behind the mouth, is also significant; for by the theory here developed both of these situations were morphologically external to the body of the polychaete and arthropod ancestor. Goodrich said (1909, p. 192) that the opening of Hatschek's nephridium into the atrium canal is to be explained. Our theory is its explanation.

As to the Tunicata, they are so degenerate that they need hardly be considered here. Young however, who derives the phylum from a sessile pelmatozoan, believes that it passed through a further sessile stage as a fixed tunicate. Berrill's views are near to these, for he derives the vertebrates directly from the tunicate larval tadpole. But there is no need to put our origin quite so low.

The complicated branchial skeleton of *Petromyzon* can be regarded as secondary; that of its ammocoete larva is much more simple. The complication would perhaps accompany the reduction of the "gill-slits" to round orifices.

24. DEPLOYMENT OF THE EARLY VERTEBRATES: 20TH CENTURY THEORIES

Nothing better illustrates our past, if not our present, ignorance of the phylogeny of the lower vertebrates than the extreme variety of the phylogenetic "trees" that have been constructed to represent their supposed relationships. Dean (1895, p. 282–3) collected seventeen of them and added his own (p. 16,98,166). He avoided discussion of the origin of the vertebrates, but supposed that the larva of *Amphioxus* suggested an early type. Since then, the production of phylogenies has continued, though it fell off through discredit. Lately, however, several have appeared. Though all may be wrong, they are useful if only to indicate at a glance the writers' opinions.

Before and at the beginning of the century there was already a general consensus of opinion that the cyclostomes were the lowest of fish-like animals, and that the elasmobranchs lay near the root of the gnathostomes. Balfour (1880) expressed this latter view, which was also that of Rabl (1889), Haeckel (1893), Dean (1895) and Smith-Woodward (1892, 1899). The ancestral elasmobranch Dean places far back in Precambrian time (p. 98), and the ancestral teleostome (p. 166) is also placed similarly early. At that time the ostracoderms were presumed to include the Antiarchi, the elasmobranchs the Acanthodii, and the dipnoi the Arthrodira.

During this century owing to exhaustive researches using several new techniques, views have greatly changed. Knowledge of the ostracoderms has been enormously extended by Stensiö, Kiaer, Heintz, White, Robertson, and many others. Stensiö was able to show how very close were the comparisons that could be instituted in the crania of cephalaspids and *Petromyzon*, thus proving their close relationship. He also did much to establish the Placodermi as distinct from the Elasmobranchii, and included in it the Antiarchi. Heintz, Broili, Gross, Watson and others built up our knowledge of this great armoured fossil group. Then Watson (1937) claimed that the gnathostomes exhibit two grades in development of the mouth, and he distinguished a new and lower subclass of gnathostome, the Aphetohyoidea, of which the Acanthodii are the most primitive, and in which the mouth skeleton is constituted only by the mandibular arch without the association of the hyoid. Into this subclass he gathered orders which at the beginning of the century were widely spread—the Acanthodii from the Elasmobranchii, the Antiarchi from the Ostracodermi, and the Arthrodira from the Dipnoi; and his claims have been generally accepted.

Watson (1937) would derive the Aphetohyoidea from an agnathous ancestor, and from the former would derive all the higher gnathostomes which include the Chondrichthyes or elasmobranchs and the Osteichthyes from which arose all the tetrapods. The origin of the last has also been a subject of constant research by many. This view of the deployment of the vertebrates is

very widely held and is combined with the popular theory of derivation of the stock from the echinoderms, and with dates of origin of the groups based on their appearances in the known palaeontological record. The four latest phylogenies known to the writer are all of this character, namely, Romer (1933, 1945), Heintz (1939), Gregory (1950) and Young (1950). They all contrast greatly with the views of Dean (1894) as well as with those of the present writer. Dean appears to have assumed that the vertebrates evolved in the sea. He did not attempt to derive them from any invertebrate, and he relegated the deployment of the divisions which he recognised to Precambrian time. Contrast this with any of the four mentioned.

According to Romer's "Family tree of invertebrates and lower chordates" (1933, fig. 11; 1945, fig. 12) two trunks arose from the coelenterates, the one yielding in succession flat worms, rotifers, molluscs, annelids and arthropods, and the other yielding in succession "round worms" (presumably Nemertea: Hubrecht, 1883; Lankester, 1910), echinoderms, acorn worms (Enteropneusts), *Amphioxus*, tunicates and vertebrates. *Amphioxus* is represented as progressive but the tunicates as retrogressive. A further tree of Romer's (1933, fig. 12; 1945, fig. 13) represented the Agnatha as yielding the three subclasses of gnathostomes in the Silurian. This is very similar to a "tree" by Haldane & Huxley (1927), who gave a single trunk from Coelenterata in place of Romer's two.

A paper by Gregory (1950) is interesting. He states (1950, p. 166) that "the supposed homologies of arthropod cephalic appendages with vertebrate gill arches rest on no good evidence." He derives the chordate stem in closest association with Echinodermata and Brachiopoda from Coelenterata in Precambrian time; whereas another, but most contrasted, branch from the coelenterates divides, also in the Precambrian, into 2 branches, the one further subdividing into Onychophora, Annulata and Mollusca, the other into Crustacea, Trilobita and Merostomata. In his system, the Onychophora in Ordovician-Silurian time give origin to the Myriapoda and Insecta! The arthropods are there represented as diphyletic, in which one part only is associated with the Annulata. The single chordate stem in the Middle Cambrian Gregory divides into Protochordata, Ostracodermi and Gnathostomata.

Young too (1950, p. 75,170,228), though he is not concerned with the annulates and arthropods, gives detailed phylogenetic trees of the chordates and related groups of animals. Up from their common ancestor back in the Precambrian came the associated stocks of the Chordata and Echinodermata, Polyzoa and Brachiopoda. The Chordata divided only in the Upper Cambrian into the Tunicata, Cephalochordata and the Agnatha which gave off in the Ordovician the gnathostome branch, so that the Acanthodii date from the Ordovician and the elasmobranchs date from the Silurian. But Young's origin of the chordate line has already been given (see sections 2, 8, 23).

These phylogenies are obviously based largely on the known fossil finds, as if the finds indicated adequately the life of the past and as if no time was required for the evolution of a new type before its appearance. To these four repetitions of both the popular zoological theory and the palaeontological theory, the one here advanced is greatly opposed. It is recognised by zoologists and palaeontologists that the different classes of "fishes"—the Cephalaspida, Anaspida, Pteraspida, Aphetohyoidea, Chondrichthyes and Osteichthyes—are all strongly contrasted with one another, without any known intermediate forms (Moy-Thomas, 1939, p. 1). The intensive work on them this century in so many lands has not at all filled up the great gaps between them. The characters that they have in common are derived from organs which they all inherit from their annulate or prot-arthropod ancestors. These "fish" classes all evolved in river basins (contrast Young, 1950, p. 125). These, even when neighbouring, were not in communication with one another. They entered the common ocean from different stream mouths, and, except that neighbouring basins lost and gained relative to one another, they remained distinct for an extensive geological time. If our theory of origin of the vertebrates be accepted, the marine ancestors of the vertebrates can be expected to have invaded the land waters by

several river mouths. But the environments in the waters of those different drainage basins would differ very much more than would the ocean off their mouths, both in temperature and in mineral content, and therefore also in life. To these different environments of different river basins, intensified by effects of geography, latitude and time, we can best attribute the divergences which the early fishes exhibit. In many cases their characters were developed under very limited competition; only after geographical changes had put river basins into communication with one another would they be able to invade new areas and come into competition with the indigenous faunas. To this we can attribute the successive invasions of new types into the known freshwater deposits of the Devonian.

Not only do palaeontologists and, following them, zoologists accept the known appearances of different fishes as the order of their evolution, but following Jaekel and Stensiö they claim that bone is especially primitive in fishes and that in those that are devoid of bone, like the modern cyclostomes and the Chondrichthyes, the primitive bone of the ancestors has been lost. For such a view there is hardly sufficient reason. As a rule a fossil fish is found because it had a resistant and durable skeleton, external or internal or both. Had it not had a skeleton it probably would not have been fossilised. In early times there were probably far more fishes without strong skeletons than with them. *Jamoytius*, described by White (1946), is one example; the Coelolepida are others. We can well imagine that from a soft fish the Chondrichthyes were evolved in a river basin, the water of which had very little lime; and once evolved, they did not later diverge appreciably in this respect. In some other basins with abundant lime the secretion of lime salts would be favoured and bone was developed. This was especially the case in benthonic forms where the exoskeleton may well have had survival value as Romer (1946) suggested. As above stated, explanations of the abundance of bone in early fishes have been advanced by H. W. Smith and Berrill (see section 18).

In opposition to Gregory, who regards the pteraspids as "amazingly primitive fishes," the writer claims them as highly specialised Agnatha. Because Heterostraci first appear in the Middle Ordovician, they suggest an antiquity for the Agnatha extending back well before the Cambrian. And if the relations between Agnatha and Gnathostomata are as above claimed (see section 16), the different types of the latter have also probably a correspondingly great antiquity, as Dean represents. The writer thus believes that Dean was right in this; also that the ancestors of all these different main branches of the vertebrates entered the land waters in Precambrian time, and required a long time for evolution before their first known occurrences. The lack of competition between the inhabitants of different river basins was probably an important factor in the evolution of so many contrasted types, and especially of the armoured benthonic forms.

A theory which involves the evolution of the Palaeozoic vertebrates has been advanced by Heintz in his paper, "How the Fishes learned to Swim" (1935); and it has been supported successively by Gregory & Raven (1941) and by Westoll (1945). Derived from study of the armoured ostracoderms and placoderms, it claims that all the higher chordates were derived from "tadpole-like" forms, and that they evolved swimming organs largely in Devonian and later times. Starting with the Agnatha: in the Osteostraci Heintz sees a progressive line from *Trematapis*, his most tadpole-like form, through *Kiaeraspis* to *Cephalaspis*, and he contrasts these with the Anaspida which were good swimmers. He claims that successive Osteostraci exhibit reduction in weight of armour. Similar changes are claimed for the Pteraspidomorphi. Again in the Arthrodira (primitive gnathostomes) he traces a series of forms improving in swimming organs, in body-form and in reduction of armour; and he states, "This group also starting from typical bottom forms gradually conquered the ocean and learned to swim." Further, after specifically extending his theory to the teleostomes, he adds that "the oldest fish-like forms and fishes were primarily bottom-living," and "were not derived from free-swimming ancestors."

These views were extensively repeated in his review of the early vertebrates (Heintz, 1938). They are largely based on those of

Stensiö, who, finding that the bony head of *Cephalaspis* proved to be closely comparable in anatomy with that of *Petromyzon*, and especially its larva *Ammocoetes*, and impressed also by the bony shields of the placoderms, claimed that in vertebrates bone was an especially primitive skeletal material, and had been reduced, and indeed lost in such descendants as the modern lamprey. This view, it was thought, was supported by the reduction in the amount of bone in the geological history of cephalaspids, pteraspids, placoderms and fishes. Regarding the origin of the chordates, Heintz espoused the popular view (1938).

25. HEINTZ THEORY AS ELABORATED BY GREGORY & RAVEN (1941)

Gregory & Raven (1941) wholeheartedly adopt the Heintz theory, but they elaborate it and extend it back to the origin of the vertebrate, so that it becomes almost directly opposite to much of the writer's sketched above. Their views are given in the quotations below. Gregory too had already espoused the popular view as to the origin of the vertebrate (1936), and elaborated it in 1950.

"The earliest chordates . . . were somewhat dorso-ventrally compressed, clinging to a rocky bottom and sucking in small food by respiratory action of the throat." "The ostracoderms were the diversified descendants" (Gregory & Raven, 1941, p. 290). Among these, the Anaspida were "fish-like derivatives of the cephalaspid stock" (p. 283).

The Anaspida display the beginnings of paired fins (p. 276): "both the pectoral and the pelvic fins were part of a series of paired projections (spines) which may at first have enabled the fish to cling to the rocky bottom of fresh-water streams" (p. 283).

"Paired fins had begun to develop as horizontal ridges, and the position of the future endoskeletal shoulder-girdle was already determined by the transverse septum behind the pericardium" (p. 283).

Ostracoderms gave rise to the gnathostomes (p. 276). "The pteraspid ostracoderms, with well-armored cephalo-thorax, instead of being aberrantly specialised, are really amazingly primitive fishes: that from their cephalo-thoracic shield, or something fundamentally like it were derived the dermocranium and the dermal pectoral girdle of all later fishes" (p. 337).

"The covering plates of the pectoral girdle of placoderms and true fishes have been derived by reduction from the thoracic armour of ostracoderms, just as the covering plates of their skulls have been derived from the cephalic plates of ostracoderms" (p. 276).

Gregory & Raven accept Heintz's view that acanthaspids are primitive among the Placodermi and claim the same armoured condition as primitive for the true fishes (p. 276).

"Median and paired fins were developed, especially as an aid in free-swimming, predaceous habits. A primitive sort of paired pectoral fins . . . was evolved among Cephalaspidomorphi" (p. 290).

"Among the earliest gnathostomes the metameric muscles early pushed their way into the base of the paired and median fin projections" (p. 291). It seems probable that these "were not continuous 'fin-folds' but nodally placed, compressed ridges strengthened anteriorly by denticles or scales which often coalesced into fin spines" (p. 290).

"In the evolution of pectoral fins the exoskeletal parts of the primitive fin projections, including spines and dermal rays of various types, to some extent preceded the development of radial rods" (p. 337).

"The 'tri-basic' pectoral, with fan-like base, . . . is the primitive type for all gnathostome fishes" (p. 337). "The long-based 'orthostichous' pectoral [of] . . . *Cladoselache* . . . has been derived from a more normal, short-based, tribasic type" (p. 291).

Regarding the origin of the shoulder girdle they finally conclude "that the so-called cartilaginous shoulder girdle is . . . merely a median process of the basal cartilages of the pectoral fin, just as the pelvic rods represent medial processes from the base of the pelvic fin" (p. 337).

Westoll also fully supports Heintz in regard to the evolution of swimming capacity in Osteostraci and in placoderms; and in part extends its application to the Acanthodii.

Describing a new cephalaspid, *Hemitele-*

aspis heintzi Westoll he suggests (1945a, p. 356) that the lateral and dorsal fields of the osteostracan head-shield are not electric organs (Stensiö), but sensory organs, probably receptors for vibratory stimuli. And he claims that the cephalaspid bony exoskeleton with the possible exception of a superficial layer of denticles was ossified only at full growth. In this connection he suggests (p. 356) "that *Cephalopterus pagei* Powrie, long regarded as a species of the Coelolepid *Thelodus*, is probably an 'unossified' Cephalaspid." Also, following Zych, he applies the same idea to Heterostraci (p. 348, 354), and sees in some more fusiform species of "*Thelodus*" unossified pteraspids.

Westoll (1945a, p. 350) regards "*Trematapis* and *Dartmuthia* as phylogenetically primitive forms which had not developed paired fins," and he suggests two possible trends of evolution by the posterior part of the great shields becoming broken up into moveable segments and moveable pectoral fins, both leading to *Cephalaspis*. He sees in the cornua of the latter's head shield the analogue of gliding planes and in the moveable pectoral fins landing flaps ("ailerons"). And he doubtfully suggests (p. 351) that in *Trematapis* the lateral fin folds are *in statu nascendi*.

In his second paper of the same year (1945b, p. 383) Westoll states that Heintz was thoroughly justified in his contention that mobile pectoral fins were developed within the Arthrodira; and after reviewing other groups he states (p. 395) that the evolution of mobile controllable paired fins from stiff-jacketed structures has taken place independently in Acanthodii and Placodermi and in the latter independently in Brachythoraci and Rhenanida and similarly in cephalaspids. Westoll further suggests that paired fins may have arisen independently in several different groups of early vertebrates, and that some pteraspidomorphs never acquired them.

26. DISCUSSION OF THE HEINTZ THEORY AS ELABORATED BY GREGORY & RAVEN AND BY WESTOLL

It is well to try to realise the essential dynamics involved in the life of the different kinds of primitive "fish"—in other words their adaptations to their physical environment. The author has above (section 2, 3, 14–17) worked out the derivation of the organs of locomotion, but he has not fully discussed the bearing of the absence or presence of a swim-bladder. As vertebrates arose, the writer still believes, in fresh waters, the effect of the greater density and composition of the ocean can here be ignored.

In the Elasmobranchii a swim-bladder is absent and they must either swim or subside to the bottom, where they can repose. But owing to their specific gravity approximating that of sea water, a very slight motion combined with the use of their paired fins as "vol planes" is sufficient to maintain their level. In the absence of a swim-bladder they are not unstable.

Similar relations would also have prevailed in ostracoderms and placoderms (Aphetohyoidea). In those having bony shields, however, the density would be higher. Both the presence of these shields and their higher density must be closely connected with the fact that the fish are built for habitually lying on the bottom; hence, it is claimed that the armour is secondary not primary.

Related to the benthonic Osteostraci (Cephalaspida) and within the same major group of ostracoderms (Monorhina) are the Anaspida. These had such flexibility that they must have already been excellent swimmers long before Devonian time. Heintz, however, puts them at a low stage because they lack organs of equilibrium; yet in the absence of a swim-bladder, they would not need them. They would spend their time swimming and resting on the bottom, for which latter they are supremely adapted by their triangular cross-section (Bulman, 1930) and their pectoral spin s. Pectoral fins are not here needed for balance, as they are in the higher fishes, which, owing to the position of their swim-bladder and backbone, are in unstable equilibrium and repose up in the water instead of on the bottom. Anaspida were already well fitted for swimming, turning, rising and sinking. It is suggested (section 16) that they swam near the surface. They may also at will have brought themselves to the density of the water by ingesting air, and may have expelled it when they desired to sink. The existence of the Anaspida strongly suggests

that the ancestors of the cephalaspids had no need to "learn to swim." In their youth they had already done so.

In the Actinopterygii and Choanichthyes, on the other hand, we have two later developments—the lungs or swim-bladder and the bony vertebrae. Owing to the fact that the two changes mentioned introduce a centre of buoyancy *below* a centre of gravity, the fish is unstable and must maintain its balance by muscular action. Hence the pectorals acquired a new function, that of maintaining balance, quite a different function from that in the distant ancestor. This is one of their main functions, others being stopping, turning laterally, and vertically; but in forward swimming except at the start they usually take no part, being held close to the body so as not to retard it. This view is however quite different from that expressed by Heintz (1935, p. 226), who mentions the dorsal and anal fins and frequently the ventrals as organs of equilibrium, and for the pectorals mentions only the function of steering.

The other general criticism which the writer would make is that the imperfection of the palaeontological record is not sufficiently considered. The writer claims on the contrary that all these forms were secondarily benthonic, and in some cases had lost the paired fins. It is possible too that the sharing of their habitat with the carnivorus eurypterids had a part in their development of armour, as Romer claimed. Following H. W. Smith and Berrill mentioned above (section 18), one can attribute their development of excessive bone to the chemical change from sea water to that of an upland lake; and one can add that perhaps in their case the change was too rapid for any other evolution.

But in their youth they would all be good swimmers and any advance that any of these groups made in swimming is to be referred to neoteny. In the light of the author's theory the significance of these ancient fishes for evolution is very different from that advanced by Heintz.

Osteostraci. The Heintz theory is opposed by the present author's principles VII, VIII, IX and X (see section 3). According to Heintz, evolution in the Osteostraci was from *Trematapis* through *Kiaeraspis* to *Cephalaspis*, or of that type; and according to Gregory the Anaspida would be the fish-like derivative of the cephalaspid stock, instead of both being derived from a common very early stock.

But the Osteostraci, highly segmented and the most primitive of ostracoderms, exhibit the primitive form of their segments between the head and tail (principle IX). We can assume with confidence that the ancestor had a body composed more extensively of such segments, i.e., even further removed from a tadpole in form.

In *Kiaeraspis* it is manifest that behind the cornua numerous segments have been added to a short *Cephalaspis*-like head. These segments have lost both their mobility and their ventro-lateral scales or pleura; and it will surely be agreed that the same process in fuller measure is responsible for the proportionally great buckler of *Trematapis*.

But this suggested evolution is the opposite of that envisaged by Heintz and by Westoll; and evolution is not reversible. Subsequent to the divergence which led towards *Trematapis*, the *Cephalaspis* line evolved its pectoral fins or paddles. From their position and from comparisons with the fins of true fishes, these were almost certainly initiated by the coalescence of ventro-lateral and latero-ventral scales which constitute pleura. Heintz (1939a, p. 101) illustrates stages in the evolution of these pectoral fins within the Hemicyclaspinae.

It cannot be doubted that *Kiaeraspis*, *Trematapis* and others with great shields acquired them by the addition of the exoskeletons of numerous normal body segments with the primitive head shield. Westoll, however, claims *Trematapis* and *Dartmuthia* with their great shields as "phylogenetically primitive forms" leading by two possible trends of evolution through other genera to *Cephalaspis*. This involves progressive breaking up of the shield into moveable segments, each of typical primitive form and furnished anew with ventro-lateral scales, which had previously been suppressed. It is entirely opposed to what we know of evolution. And not only this, but he also claims that out of the shield the moveable paddles of *Cephalaspis* were evolved. The writer cannot believe that there is any truth in the supposed osteostracan phylogenies of Heintz or Westoll.

If we consider how the Osteostraci must have lived, we can better understand their differences. From their shape we infer that they were benthonic creatures spending most of their time on the bottom. Nevertheless, water still had to freely enter the mouth carrying both oxygen and food; and it went out by the gill openings, after suspended food had been filtered off and the blood in the gills had been oxygenated. Free channels must have been present for this water to enter in front and to escape behind.

In *Cephalaspis* the bottom of the shield is flat or concave, with the mouth near the front and the paired gill openings as well as the mouth disposed in a large circle within it; hence, special provision must have existed for a water space beneath it. On the other hand, the elevated eyes suggest that the shield may have been habitually half buried in the sediment. The short shield was well-shaped for ploughing through the sediment, when the creature was swimming at the bottom.[1] The writer imagines, therefore, that the necessary clear water space beneath the fish was made in that way, and the rearward channels and currents may have been initiated and perhaps partly maintained by continuous motion of the pectoral fins. Perhaps this was not their only function. Westoll suggests that in swimming they acted as landing flaps or ailerons.

In *Trematapis* there are no paddles; but the much more extensive ventral surface of the buckler is highly convex. Consequently, it seems probable that, when the creature settled on the bottom, its gill openings as well as its mouth were already exposed, and as there are no pectoral fins, that ciliary and muscular action within the cephalon were sufficient to maintain the currents.

This consideration of *Cephalaspis* and the possible origin and function of its paddles suggests that in the ancestors of the known Osteostraci a function of the anterior pleura or fins may have been to maintain by their motion a rearward current on each side when the creature was lying on the bottom. In *Trematapis* such a function had become unnecessary.

That the Osteostraci were only secondarily benthonic is not only indicated by the character of their primitive segments, but is strongly supported by the contemporaneous existence of the related Anaspida.

The Osteostraci in their post-cephalic body, composed as it is of such a great number of similar segments, all provided with "pleura," are as stated above much the most primitive of the ostracoderms. This may be attributed to their having early taken to a benthonic life, which, although causing great modification of the anterior part of the body, left the rest relatively unaffected.

Westoll's suggestion that they developed armour only after full growth is very welcome. In their early larval stages they would have been purely nectonic. If this is proved, it will strongly support the present writer's view that the benthonic life was secondary, not primary, as is claimed by Heintz, Gregory and Westoll.

PTERASPIDA. By our theory these are very much less primitive than the cephalaspids, and include very highly specialised forms like *Anglaspis* and *Poraspis* (text-fig. *6a–f*) in which segmentation is excessively reduced, though in the single lines of ventrolateral scales we sometimes still have vestiges of the pleura (Kiaer, 1932, p. 13, 19, 20). For example, *Pteraspis* itself (text-fig. *5a,d–g*), instead of being "amazingly primitive Fishes," are extremely specialised, as we find from White's memoir (1935, p. 440, 454). Although the fish indeed looks like a compound in equal parts of two very different animals, it is throughout beautifully streamlined. The head half is completely armour-plated with the anterior half rising continuously to the front, and with a single pair of gill openings behind; the tail half, which constitutes the power unit, is covered with a flexible armour of rhomboid scales, whereby the primitive segmentation is quite masked, and the primitive "pleura" are lost. Every one of these features indicates high specialisation. The hypocercal tail may have been handed down from surface-swimming ancestors; but, on the other hand, it functioned with the rising front to counteract the anterior extra weight of armour. "As suggested by

[1] Possibly related to this function is the fact that in *Aceraspis* the front rim of the head-shield, to right and left and both above and below, has a joint across it at the place where the width of the shield is half that of the full width at the cornua. This suggests that the section in front was moveable upon the rest (Heintz, 1939).

Zych (1931) the plates of the carapace were not formed until a relatively late stage, and at first were not in contact with one another" (White, 1935, p. 455). See also *Poraspis* (our text-fig. *6a-f*). Behind the "head" eleven rings of scales indicate that further number of segments, in front of the more irregular scales of the tail, which might comprise another dozen segments. Each definite ring of the eleven consists of six scales: a medio-dorsal, a medio-ventral, and on each side a lateral and a ventro-lateral, which on each side represents the ancestral pleuron. Instead of being "amazingly primitive," it is amazingly specialised.

By their form these genera are fitted both for swimming and for repose on the bottom, for, when at rest, the convexity of their ventral shield elevated both the mouth and the gill openings well up in the water. Because it had no swim bladder and was extensively encased in heavy bone, the pteraspid rested lying on the bottom, and therefore needed no pectoral fins. Their absence, on this view, is evidence of a higher, not lower, grade of evolution. Great error, the writer thinks, results from overlooking the extreme imperfection of the palaeontological record. It leads to claims of evolutionary series through the few fossil fish which are known. The geological record is extremely incomplete, and is mostly a record of marine conditions, whereas the vertebrates originated in fresh water. The imperfection of the palaeontological record is superposed on that of the geological. Each fossil fish is a record of fortunate burial, mineralisation, survival, and exposure. The vertebrate fossils of later Palaeozoic time in relation to the vertebrate life they represent can be likened to a "drop in a bucket," and those of the older Palaeozoic to a "drop in the ocean," whereas those of Cambrian and Precambrian time are altogether unknown. The claims of Heintz and Westoll are open to this criticism. The writer does not consider their phylogenies logical, even those parts that are not in opposition to basic principles. Should there be truth in the Heintz phylogenies within the placoderms, it must be remembered that they did not need to "learn to swim," for in their youth they had all done it. All that was needed was for swimming to be continued into the adult life. This is equal to saying that they were only secondarily benthonic. The armoured ostracoderms and placoderms however were claimed by Heintz as primarily benthonic, and this is fully accepted by Gregory & Raven and by Westoll. But just as the claim has been made above that the Osteostraci were only secondarily benthonic, so the same claim is made here for the placoderms. And similar arguments can again be adduced, viz., that:

I. The primitive part of the body is behind the head and suggests a fish-like, not a tadpole-like nor an armoured, form.

II. Placoderms were contemporaries of the Acanthodii, and by Middle Devonian, besides these, of various Crossopterygii, Dipnoi and Palaeoniscoidea (which except for their dominantly heterocercal tails, offer no suggestion of benthonic character). All of these indicate the great antiquity of free swimming in their ancestry.

III. The occasional finds of soft-bodied chordates, i.e., with less skeleton than the well known Anaspida (e.g., White 1946; and *Palaeospondylus* and *Thelodus*) and the fact that the fossil fishes illustrate the evolution of size, suggest the existence of abundant small soft-bodied fishes in the Palaeozoic fresh waters, from which abundant types of fish can more easily be supposed to have evolved.

Returning to the question of phylogenies within the fishes, Gregory & Raven claim that the ostracoderms gave rise to the placoderms and the higher fishes. Such a lineage is very improbable, for the arthropod appendages which, as explained above (section 16), became the jaws of the gnathostome, have in the ostracoderm developed in a very different way, and could not change into jaws. Again, evolution is not reversible (principle X). Furthermore, the gnathostomes appeared so early and at that time already exhibited such great diversity, that they must have had a great antiquity.

All four writers here discussed claim, too, that median and paired fins arose *de novo* within these chordates, the paired fins in Devonian and later time. Further, it is implied that these arose independently in several different orders, and this is indeed specifically stated by Westoll. This claim has already been sufficiently answered.

Their phylogenies have not been proved; and if in any lineage paired fins did appear, this can be attributed to neoteny.

27. EVOLUTION OF THE VERTEBRATES: BRIEF REVIEW

Evolved in the rivers of Precambrian time, the early aquatic ancestors of the vertebrates inhabited both the rivers and lakes of the older Palaeozoic North Atlantic continent, represented now by North America and Europe, where in the lake regions some evolved into tetrapods. Later, in the newer Palaeozoic periods, others of them extensively migrated to the ocean.

Recent evidence has enabled palaeontologists to trace extensively the evolution and deployment of the vertebrates through post-Silurian time. It reveals countless revolutionary changes. The successive environments changed for the vertebrates their foods and habitats, and these brought in their train changes in locomotion, body-chemistry, and physiology. The vertebrate habitats included water, land, and air, not only within each but also at their mutual boundaries. For example, from water some migrated to a habitat of land and air, and many of these returned to water. These involved changes in locomotion, through all the media—water, land and air—as well as at their bounding surfaces. Such migrations are most strange, but the evidence is ample. In view of this, the great revolutionary changes envisaged in this "Outline" need not be denied because they violate this or that biological principle. Nature was not bound by any man-made theories, and she has had colossal time in which to effect her evolutions and revolutions.

Comparative studies in morphology, ontogeny, and phylogeny enable us to trace the evolution of the vertebrate up from the Protozoa through Coelenterata, Annelida, primitive Arthropoda and primitive Vertebrata to man. The course of evolution has been so complicated, and in so many different directions at different times, that nature has completely removed vast sections out of the ontogenies. It is perhaps because a great pre-vertebrate section has been eliminated, that it is so difficult to trace this great evolution.

The theory here presented claims to indicate those characters in vertebrates and lower chordates which are primitive, and those which are secondary or derived. If it is accepted as substantially correct the theory will lead to a complete change in present concepts of the early evolution of the vertebrate. It should also have important effects in zoological classification. The Vertebrata or Chordata should not be separated from the Appendiculata by the Echinodermata as is almost universal; nor by these and the Brachiopoda, Polyzoa and Mollusca, as is frequent. The Chordata or Vertebrata become the highest phylum of the great superphylum Segmentata. Also, as the lower chordates are all obviously degenerate, Vertebrata is a much better name for the phylum than is Chordata, which should therefore be dropped in favour of Vertebrata.

It would be strange if in so complicated a subject no mistakes have here been made; but the writer hopes that his paper will be followed by more intensive work by others much better qualified and that it will lead to a rapid solution of a problem, which has long remained obscure.

Finally, the writer would express his great indebtedness: first to Gaskell, whose book "The Origin of Vertebrates" he first read so very long ago, and who deserved better of posterity than he has so far received; secondly to those vertebrate specialists who so kindly criticised the first and the second drafts of this paper and helped him to literature, namely Prof. T. S. Westoll and Prof. Sir J. Graham Kerr; to Prof. L. J. Wills, who kindly gave access to his library and for his criticism of the present paper; to Prof. A. Heintz for the stimulus of his papers and for allowing his excellent figures to be used in illustration; and lastly to a great number too numerous to mention who also find their place among the References. Further, to those helpers who find themselves criticised, he would extend his most sincere thanks for their help and his most sincere apologies for his defection.

REFERENCES AND LITERATURE

BALFOUR, F. M., 1878, Monograph on the development of elasmobranch fishes: xi+295 p., 20 pls., London.

——, 1881, A treatise on comparative embryology, volume 2: illus., London.

BARRELL, J., 1916, Influence of Silurian-Devonian climates on the rise of air-breathing

vertebrates: Bull. Geol. Soc. America, v. 27, p. 387–436.

BARRINGTON, E. J. W., 1937, The digestive system of *Amphioxus*: Phil. Trans. Roy. Soc., London, v. B228, p. 269.

BATESON, W., 1886, The ancestry of the Chordata: Quart. Jour. Micr. Sci., v. 2, p. 26.

BERNARD, N. M., 1892, The Apodidae: a morphological study: London, Macmillan.

BERRILL, N. J., 1955, The origin of vertebrates: 257 p., illus., Oxford, Clarendon Press.

DE BEER, G. R., 1928–1951, Vertebrate Zoology: an introduction to the comparative anatomy, embryology, and evolution of chordate animals: London, Sidgwick and Jackson; New York, Macmillan.

——, 1940, Embryos and ancestors: x+108 p., 2 pls., Oxford, Clarendon Press.

DELSMAN, H. C., 1921–1922. The ancestry of vertebrates as a means of understanding the principal features of their structure and development: Nat. Tijdschr. Batavia, v. 81, p. 187–286, 19 figs.; v. 82, p. 34–89, 107–189, 3 pls., 45 figs.

DOHRN, A., 1875, Der Urspring der Wirbeltiere und das Princip des Functionswechsels: Genealogische Skizzen: xv+87 p., Leipzig, Wilhelm Engelmann.

FELL, H. B., 1949, Echinoderm embryology and the origin of chordates: Biol. Rev., v. 23, p. 81.

FERRIS, G. F., 1949, The principles of comparative morphology: Microentom. Nat. History Mus., Stanford Univ.

FORSTER-COOPER, C., 1940, In, Parker & Haswell, Text-book of Zoology, volume 2: Macmillan.

GARSTANG, W., 1894, Preliminary note on a new theory of the phylogeny of the Chordata: Zool. Anz., v. 444 (17), p. 122–125.

——, 1928, The morphology of the Tunicata and its bearing on the phylogeny of the Chordata: Quart. Jour. Micr. Sci., v. 72, p. 51–187, 16 figs.

GASKELL, W. H., 1889, On the origin of the central nervous system of vertebrates. Brain 12.

——, 1908, The origin of vertebrates: London, Longmans, Green & Co.

GEGENBAUR, C., 1876, Morphologie der Gliedmassen der Wirbeltiere.

GOETTE, A., 1895, Ueber den Urspring der Wirbeltiere: Verh. deutsch Zool. Gesell., v. 5, p. 12–30.

GOODRICH, E. S., 1902, On the structure of the excretory organs of *Amphioxus*, Pt. 1.; Quart. Jour. Micr. Sci., n. ser., v. 45, p. 493–501, pl. 27, 1 fig.

——, 1909a, On the structure of the excretory organs of *Amphioxus*, Pt. 2: *ibid.*, v. 52.

——, 1909b, Vertebrata Craniata, In, E. R. Lankester, A treatise on Zoology, volume 9: xvi+518 p., 515 figs., A & C Black, London.

——, 1930, Studies on the structure and development of vertebrates: 837 p., 754 figs., Macmillan & Co.

——, 1934, The early development of nephridia in *Amphioxus*, parts I and II: Quart. Jour. Micr. Sci. London, n. ser., v. 76, p. 499–510, 655–674, 6 pls., 5 figs.

GRAY, J., 1933, Studies in animal locomotion. I. The movement of fish, with special reference to the eel; II. The relationship between waves of muscular contraction and the propulsive mechanism of the eel; III. The propulsive mechanism of the whiting (*Gadus merlangus*): Jour. Exp. Biology, v. 10, no. 1, p. 88–104; no. 4, p. 386–400, 2 pls., 5 figs.

GREGORY, W. K., 1933, Fish skulls: A study of the evolution of natural mechanisms: Trans. Amer. Philos. Soc., n. ser., v. 23, pt. 2, p. 75–481, 302 figs.

——, 1936, The transformation of organic designs: a review of the origin and development of the earlier vertebrates: Biol. Rev., v. 11, p. 311–344, 10 figs.

——, 1950, Evolution in vertebrates and arthropods: Evolution, v. 4, no. 2, p. 164–171.

——, 1951, Evolution emerging: Amer. Mus. Nat. History, New York (2 volumes).

—— & RAVEN, H. C., 1941, Studies on the origin and early evolution of paired fins and limbs, parts I–IV: Ann. N. Y. Acad. Sci., v. 42, p. 273–360, 4 pls., 34 text-figs.

GROSS, WALTER, 1931, *Asterolepis ornata* Eichw. und das Antiarci-Problem: Palaeontographica Stuttgart, v. 75, p. 1–62, 12 pls., 24 figs.

——, 1935, Histologische Studien am Aussenskelett fossiler Agnathen und Fische: Palaeontographica Stuttgart, ser. A., v. 83, p. 1–57, 7 pls., 7 text-figs.

HAECKEL, E., 1876 & 1906, The history of creation: Translation revised by Lankester: Paul, Trench, Trübner & Co., London.

HALDANE, J. B. S., & HUXLEY, J., 1927–1945, Animal biology: Oxford, Clarendon Press.

HARRIS, J. E., 1936, The role of the fins in the equilibrium of the swimming fish: Jour. Exp. Biology, Edinburgh, v. 13, p. 476–493, 8 text-figs.

——, 1937, The mechanical significance of the position and movements of the paired fins in the Teleostei: Papers Tortugas Lab., v. 31, p. 171–189, 8 text-figs.

——, 1938, The rôle of the fins, etc. II. The rôle of the pelvic fins. Jour. Exp. Biology, v. 15, p. 32–47, 8 text-figs.

HEBERER, G., 1954, Die Evolution der Organismen Ergebnisse und Probleme der Abstammungslehre, 2nd ed.

HEINTZ, A., 1935, How the fishes learned to swim: Smiths. Inst. Rept. for 1934, p. 223–245, 12 figs.

——, 1938, Ueber die ältesten bekannten Wirbeltiere: Die Naturwiss. Berlin, v. 26, no. 4, p. 49–58, 4 figs.

——, 1939a, Die Entwicklung des Tierreichs: *Ibid.*, v. 27, no. 14, p. 223–226, 2 text-figs.

——, 1939b, Cephalaspida from the Downtonian of Norway: Skr. Norsk Vitensk.-Akad. Oslo, 1 Math. Nat. Kl., no. 5, 119 p., 30 pls., 35 figs.

HOLMES, A., 1947, The construction of a geological time scale: Trans. Geol. Soc. Glasgow, v. 21, no. 1, p. 117.

HOLMGREN, N., & STENSIÖ, E. A., 1936, Kranium und Visceralskelett der Akranier, Cyclostomen und Fische: Bolk. Handb. vergl. Anat. Wirbeltiere, v. 4, p. 223–500, text-figs. 203–373.

HOPPE E. H., 1931, Die Coelolepiden und Acan-

thodier des Obersilurs der Insel Oesel, Palaeontographica, v. 76, p. 63–90, Stuttgart.
HUBRECHT, A. A. W., 1883, On the ancestral form of the Chordata: Quart. Jour. Micr. Sci., ser. 5, v. 23, p. 349–68.
JORDAN, D. S., 1905, A guide to the study of fishes, volume 1; xxvi+623 p., illus., New York, A. Holt & Co.
KERR, J. G., 1907, The work of John Samuel Budgett: Cambridge University Press, 195.
——, 1919, Text-book of embryology, volume 2: Macmillan.
——, 1921, Text-book of zoology for medical students: Macmillan.
——, 1945, Vertebrata and vertebrate embryology: Encyc. Britt., 14th ed.
KIAER, J., 1924, The Downtonian fauna of Norway. I. Anaspida: Skr. vidensk. selsk, Mat. Nat. Kl. Kristiania, no. 6, p. 1–139, 14 pls., 50 figs.
——, 1928, The structure of the mouth of the oldest known vertebrates, pteraspids and cephalaspids: Palaeobiologica, v. 1, p. 117–134, illus., Wien.
——, 1932, New coelolepids from the Upper Silurian on Oesel (Estonia) Arch. naturk. Estlands, v. 10, no. 3, p. 8, 2 pls., [Edited by A. Heintz].
——, 1932, The Downtonian and Devonian Vertebrata of Spitzbergen. IV. Suborder Cyathaspida: Skrifter on Svalbard og Ishavet, no. 53, p. 1–26, 11 pls., 12 figs.
—— & HEINTZ, A., 1935, The Downtonian and Devonian vertebrates of Spitzbergen: 5, Cyathaspida.
KOZLOWSKI, R., 1947, Les affinités des graptolites: Biol. Rev. Cambridge, v. 20, p. 93–108, text-figs.
LAMARCK, J. B., 1815, Histoire naturelle des animaux sans vertèbres.
LAMEERE, A., 1891, L'origine des vertébrés: Bull. Soc. belge Micr., v. 14.
——, 1905, L'origine de la corde dorsale: Ann. Soc. R. Malac. belge, v. 40.
LEACH, W. J., 1944, The archtypal position of *Amphioxus* and *Ammocoetes*, and the role of endocrines in chordate evolution: Amer. Nat., v. 78, no. 777, p. 341–357.
LOCY, W. A., 1895, Contribution to the structure and development of the vertebrate head: Jour. Morphology, v. 11, p. 497–594, pls. 26–30, figs.
MATTHEW, W. D., 1915, Climate and evolution: Ann. N. Y. Acad. Sci., v. 24, 171.
MILLER, A. K., CULLISON, J. S., & YOUNGQUIST, W., 1947, Lower Ordovician fish remains from Missouri: Amer. Jour. Sci. v. 245, no. 1, p. 31–34, 1 pl.
MINOT, C. S., 1897, Contribution a là détérmination des ancêtres de vertébrés: Arch. zool. expér. et gen., v. 3, p. 5.
MOY-THOMAS, J. A., 1938, The problem of the evolution of the dermal bones in fishes: Essays on Evolution, edited by G. R. de Beer, Oxford.
——, 1939, Palaeozoic fishes: 149 p., New York, Chemical Publ. Co., Inc.
——, 1939, The early evolution and relationships of the elasmobranchs: Biol. Rev., v. 14, p. 1–26, 12 figs.
——, 1940, The Devonian fish *Palaeospondylus gunni* Traquair: Phil. Trans. Roy. Soc. B, v. 230, p. 391.
—— & WHITE, E. I., 1939, On the palatoquadrate and hyomandibula of *Pleuracanthus sessilis* Jordan: Geol. Mag., v. 76, no. 904, p. 459–463, 4 figs.
NORMAN, J. R., 1936–1947, A history of fishes: London, E. Benn.
ORTON, J. H., 1913, The ciliary mechanism on the gill and the mode of feeding in *Amphioxus:* Jour. Mar. Biol. Ass., v. 10.
PATTEN, WILLIAM, 1890, On the origin of vertebrates from arachnids: Quart. Jour. Micr. Sci., v. 31, p. 317–378, pls. 23, 24.
——, 1912, The evolution of vertebrates and their kin: xxi+486 p., 309 figs., Phila., P. Blackiston's Son & Co.
FERRIER, E., 1898, Affinité des vertébrés: Traité de zoologie, v. 6, p. 23, 57.
RAW, FRANK, 1925, The development of *Leptoplastus salteri* and other trilobites, etc.: Quart. Jour. Geol. Soc. London, v. 81, p. 223–322, 4 pls.
——, 1927, The ontogenies of trilobites and their significance: Amer. Jour. Sci., ser. 5, v. 14, p. 7–35, 11 text-figs., p. 131–149, figs.
——, 1949, Some stages in the evolution of the nervous system and the fore-gut of the polychaet: Smithson. Misc. Coll., v. 111, no. 8, p. 1–35.
——, 1953, The external morphology of the trilobite and its significance: Jour. Paleontology, v. 27, no. 1, p. 82–129, 7 text-figs.
——, 1955, The Malacostraca: their origin, relationships and phylogeny: Ann. & Mag. Nat. History, ser. 12, v. 8, p. 731–756, 5 figs.
——, 1957, Origin of chelicerates: Jour. Paleontology, v. 31, no. 1, p. 139–192, 9 text-figs.
RICHARDSON, E. G., 1936, The physical aspects of fish locomotion: Jour. Exp. Biology, v. 13, p. 63–74, 8 text-figs.
ROBERTSON, G. M., 1935, The ostracoderm genus *Dartmuthia* Patten: Amer. Jour. Sci., v. 29, p. 323–335, 5 figs.
——, 1938, New genera of ostracoderms from the Upper Silurian of Oesel: Jour. Paleontology, v. 12, no. 5, p. 486–493.
——, 1938, The Tremataspidae 1 & 2: Amer. Jour. Sci., ser. 5, v. 35, no. 207–8, p. 172–296, 3 pls., 5 figs.
——, 1942, Some aspects of evolutionary theory: Fort Hays Kansas State Coll. Stud. 4.
——, 1949, Some contributions of fossil Study to the problem of vertebrate origin: Proc. Iowa Acad. Sci., v. 56, p. 379–384.
——, 1953, Some attempts at phylogeny of early vertebrates: Proc. Iowa Acad. Sci., v. 60, p. 725.
ROMER, A. S., 1933, Eurypterid influence on vertebrate history: Science, v. 78.
——, 1945, Vertebrate Paleontology, 2nd ed.: Chicago, Univ. Chicago Press.
——, 1946, The early evolution of fishes: Quart. Rev. Biology, v. 21, 33.
——, 1955, The vertebrate body, 2nd ed.: Philadelphia.

——, 1955, Fish origins in fresh and salt water: Mar. Biol. & Oceanogr. Res. 3, 3, 61.
—— & GROVE, B. H., 1935, Environment of the early vertebrates: Amer. Midl. Nat., v. 16, p. 805–856, 2 figs.
ST. HILAIRE, G., 1822, Discours sur l'Anatomie: Mem. Soc. Linn. Paris, v. 2.
SÄVE-SÖDERBERGH, G., 1934, Some points of view concerning the evolution of the vertebrates and the classification of this group: Arkiv för Zoologie, v. 26A, p. 1–20, 5 figs.
SEMPER, C., 1875, Die Stammverwandschaft der Wirbeltiere und Wirbellosen: Arb. Zool. Inst. Würzburg, 2.
SIMPSON, G. G., 1926, New reconstruction of *Lasanius:* Bull. Geol. Soc. America, v. 37, p. 397–402, fig.
SMITH, H. W., 1939, Studies in the physiology of the kidney: 106 p., 7 figs., Porter Lectures, ser. 9, Univ. Kansas, Sch. Medicine, Univ. Ext. Div., Univ. Kansas.
——, 1953, From fish to philosopher: Little, Brown & Co., Boston.
SÖDERSTRÖM, A., 1927, Über segmental wiederholte "Nuchal-organe" bei Polychäten: Zool. Bidrag, Uppsala.
STENSIÖ, E. A., 1927, The Downtonian and Devonian vertebrates of Spitsbergen, Part I. Family Cephalaspidae: Skr. Svalb. og Nordishavet, no. 12, p. 1–391.
——, 1932, The cephalaspids of Great Britain: 220 p., 66 pls., 70 figs., Brit. Mus. Nat. History, London.
——, 1939, A new anaspid from the Upper Devonian of Scaumenac Bay in Canada, with remarks on the other anaspids: Hemdl. k. Svensk. Vetensk. Akad., ser. 3, v. 18, 25 p., 1 pl., 7 figs.
—— & JARVIK, E., 1939, Agnathi and Pisces: Fortschr. d. Palaeontologie, v. 2, p. 254–295.
STETSON, H. C., 1927, *Lasanius* and the problem of vertebrate origin: Jour. Geology, v. 35, p. 247–263, figs.
STROMER, E., 1926, Die Entwicklung der Tierwelt: Natur. und Mensch., v. 2, p. 247.
TRAQUAIR, R. H., 1898, Report on fossil fishes in the Upper Silurian rocks of the south of Scotland: Trans. Roy. Soc. Edin., v. 39, no. 3, p. 827–864.
——, 1905, Supplementary report: *ibid.*, v. 40, p. 879.
——, 1900, The palaeontological evidence of the descent of fishes: Rep. Brit. Ass. Zoology, Bradford, 1899.
WALLS, G. L., 1939, The origin of the vertebrate eye: Arch. Ophthalmology, v. 22, p. 452–486.
——, 1942, The vertebrate eye and its adaptive radiation: Cranbrook Inst. Sci. Bull. 19, 785 p., 197 text-figs., 1 pl.
WÄNGSJÖ, G., 1952, The Downtonian and Devonian vertebrates of Spitsbergen. IX. Morphologic and systematic studies of the Spitsbergen cephalaspids: Norsk Polarinstitutt Skrift. Kongel. Industri Handverk-og Skipsfartsdep., no. 97, 657 p., 118 pls., 109 figs., Oslo.
WATSON, D. M. S., 1919, 1926, The evolution and origin of the Amphibia: Phil. Trans. Roy. Soc. London, ser. B, V. 209, p. 1–73, pls. 1–2; v. 214, p. 189–257, 39 text-figs.
——, 1925, The structure of certain palaeoniscids and the relationships of that group with other bony fish: Proc. Zool. Soc. London, p. 815–870, 2 pls., 30 text-figs.
——, 1937–8, The acanthodian fishes: Phil. Trans. Roy. Soc. London, ser. B, v. 227–228, p. 49–146, pls. 5–14, 25 text-figs.
——, 1939, The origin of frogs: Trans. Roy. Soc. Edin., v. 60, p. 195.
——, 1951, Palaeontology and modern biology: Yale Univ. Press.
WESTOLL, T. S., 1937, The Old Red Sandstone fishes of the North of Scotland, etc. Proc. Geol. Assoc., London, v. 48, p. 13–45, text-figs. 2–11.
——, 1943, The origin of the tetrapods: Biol. Rev. Cambridge, v. 18, no. 2, p. 78–98, figs.
——, 1944, The Haplolepidae, a new family of Late Carb. bony fishes, a study in taxonomy and evolution: Bull. Amer. Mus. Nat. History, v. 83, art. 1, p. 1–121, pls. 10, figs. 52.
——, 1945a, A new cephalaspid fish from the Downtonian of Scotland, with notes on the structure and classification of ostracoderms: Trans. Roy. Soc. Edin., v. 61, p. 341–357. 1 pl., 7 text-figs.
——, 1945b, The paired fins of placoderms: *ibid.* p. 391–398, 9 text-figs.
——, 1949, On the evolution of the Dipnoi: Genetics, Palaeontology and Evolution, Ed. G. S. Jepson, Princeton.
WHITE, E. I., 1935, The ostracoderm *Ptereaspis* Kner and the relationships of the agnathous vertebrates: Phil. Trans. Roy. Soc. London, B, V. 225, p. 381–457, pls. xxv–xxvii, 97 text-figs.
——, 1946, *Jamoytius kerwoodi*, a new chordate from the Silurian of Lanarkshire. Geol. Mag., v. 83, p. 89–97, 2 text-figs.
WHITEHOUSE, R. H., 1910, The caudal fin of fishes: Proc. Roy. Soc. London, v. B82, p. 134–143.
WILLEY, A., 1894, *Amphioxus* and the ancestry of the vertebrates: New York, Macmillan.
WOODWARD, A. S., 1892, The evolution of fins: Nat. Sci., v. 1, p. 28–34, figs.
——, 1932, Zittel's text-book of palaeontology, volume 2: Macmillan.
——, 1935, The affinities of the acanthodian and arthrodiran fishes: Ann. & Mag. Nat. History, ser. 10, v. 15, p. 392–395.
YOUNG, J. Z., 1950, The life of vertebrates: xvi + 767 p., 497 figs., Oxford, Clarendon Press.
ZYCH, W., 1931, Fauna Ryb Dewonu i Downtonu podola Pteraspidomorph: Heteratraci Czesc. 1A: p. 91, 9 pls., Lwow.
——, 1937, *Cephalaspis koslowskii* n. sp., from the Downtonian of Podole, Poland: Arch. Towarg. Nauk, Lwow, ser. 3, v. 9, no. 1, p. 49–96, 4 pls.

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THE ORIGIN OF THE VERTEBRATES

LEONARD R. SILLMAN, M.D.
565 Park Avenue, New York 21, N. Y.

ABSTRACT—The embryology of the vertebrates resembles that of the cephalopod much more than that of the echinoderm. The basic structuring of circulatory, respiratory, renal, and skeletal system in *Nautilus* shows marked similarities with those in the vertebrates. By contrast, echinoderms lack any distinctive basic adult vertebrate features. The transformation from a nautiloid to a vertebrate would violate no known evolutionary process, and would explain the enigmatic vertebrate pineal eye. It is proposed that the vertebrate originated from an orthoconic nautiloid cephalopod.

DESPITE the wide acceptance of an echinoderm ancestry, the problem of the origin of the vertebrates still remains one of the major "missing links" in the grand panorama of the evolution of life. Of the three major higher invertebrate phyla extant in the Cambrian from which the vertebrates might have originated in the Ordovician, the molluscs, the echinoderms, and the arthropods, only the latter two have been regarded by various authorities as having been ancestral. In recent years, the weight of most scientific authority has definitely shifted in favor of Garstang's theory (1894) of an echinoderm ancestry for the vertebrates largely on the basis of embryonic development patterns (Romer, 1941, 1949; Young, 1950), despite Fell's demonstration (1948) that the more developed echinoderm larval forms on which Garstang based his hypothetical reconstruction are in no way primitive.

Comparison of the anatomy of the various echinoderms with the classical vertebrate pattern casts even more doubt on such a linkage. For the echinoderms show no evidence of the distinctive vertebrate skeletal, circulatory, respiratory, and renal patterning and have such a primitive neural and sensory equipment that there does not seem to exist any even premonitory signs of the later high development of these structures. At the same time, no chordate shows any evidence of the highly distinctive echinoderm feature of an ambulacral system. The echinoderm, except for its coelomic structure and embryonic bilaterality and patternings, seems as far removed from any chordate as the coelenterate it so closely resembles.

The above marked morphological divergences must inevitably challenge the validity of the embryonic similarities. For one of the major features of the evolution of the larger units of the animal kingdom such as phyla and classes consists of a marked morphological similarity, particularly in the basic visceral and tissue patterning between such related groups as the annelid worm and the arthropod, the fish and the bird. The marked divergence of higher evolution and structuring, as for example the bird's wings, is based on a common basic patterning, in this instance consisting of fish-developed bone.

No basic similarity of patterning is to be found in comparing any chordate with any echinoderm. For an echinoderm to have become a vertebrate, a whole new set of genes for the creation of basic and vital tissues would have to be created *de novo*. Such a radical transformation of genetic substance is unknown in nature wherein gradualism or the relatively slow transmutation of special structures and functions has been the universal rule. A fish does not have the genes to become a mammal, but it does have the genetic equipment, as demonstrated by its morphology, to mutate in the direction of an amphibian. In regard to the echinoderms and the chordates, the basic pattern is so different that it is difficult and impossible to visualize the transformation from the former to the latter. Hence, one is left with a sense of "spontaneous generation" of the vertebrates some four to five hundred million years ago.

Despite certain resemblances such as bilaterality and a metameric patterning, efforts to demonstrate an arthropod ancestory

for the vertebrates has by now been generally discarded, despite Patten's (1912) and Gaskell's (1908) work on the behalf of *Limulus*. This leaves the third major higher invertebrate of the Cambrian, the mollusc, to be considered. Of the molluscs, the gastropods and the nautiloid cephalopods were plentiful during the Cambrian, of which the cephalopods underwent great evolutionary change during the Ordovician (Twenhofel & Shrock, 1935).

Turning first to the data of comparative embryology, we find that the cephalopod mollusc bears a closer resemblance to the vertebrate in its basic embryonic patterns than does the echinoderm. Unfortunately, inasmuch as the embryology of the Pearly *Nautilus* has not as yet been described, the only material available for comparison is that from the higher cephalopods, the Sepioidea and the Octopoda. However, it seems proper to assume that, just as with other classes in the phylogenetic tree, the embryological patterns of the lower and the higher members of the same class follow the same basic patterns.

The cephalopod egg is telolecithal, like that of all lower vertebrates, but the echinoderm egg is homolecithal, like that found in only the highest and most advanced vertebrates, i.e., mammals. Although cleavage in lower molluscs is spiral, that of the cephalopod is incomplete, as is that of the vertebrates. Echinoderms have a radial cleavage quite unlike that in any of the vertebrates. In regard to blastulation, gastrulation, and mesoderm formation, characteristics of both the cephalopod and the echinoderm patternings are to be found amid the chordates. For example, enterocoele endomesoderm formation like that of the echinoderm is to be found only in the lower chordates and not in the true vertebrate, whereas secondary endomesoderm formation, such as that in the cephalopod, is also found in the vertebrates.

All in all, both echinoderms and cephalopods share an equal number of similar characteristics with the chordates—five each (Richards, 1931). However, MacBride (1914) quotes Lankester as describing a primitive streak in the segmenting egg of the cephalopod. Thus, from the data of comparative embryology as good a case can be made for the molluscan cephalopod as the ancestor of the vertebrate as for the echinoderm. From egg structure and cleavage patterning, a better case can be made out for the cephalopod.

Garstang's relating the lower chordates with the echinoderms on the basis of the resemblances of their larvae, implying that the chordate arose by neoteny, has been one of the main bases of the echinoderm theory of chordate origination. The phenomenon of neoteny can hardly explain the emergence of new forms of life, for even if the embryos of different phyla resemble each other, the genetic equipment of each directs the final emergence of entirely different structures and functions. Except in the instance of paedogenesis, not found amid the echinoderms (De Beer, 1951), it is the mature organism, not the larvae, which manufactures germ plasm and new mutations. Therefore, the self transformation of an echinoderm larva to a lower chordate by moving bands of cilia seems highly improbable. Mutations arise in the germ plasm by changing genetic patterns capable of manufacturing adult tissues; they are not produced in the non-reproductive larvae.

Neoteny can explain certain superficial shifts in morphology, such as the contrast between apes and man, as pointed out by Bolk (1926). It cannot explain the creation of new forms for this is achieved within the chromosomes and not after fertilization wherein the embryo develops the basic forms dictated by the genes. Many similarities may be observed between the blastula and gastrula of various forms of life without there being any indication of a direct ancestry. An early human embryo looks like a worm, but this does not mean that man is descended immediately from annelids. The main evidence in descent must come from adult or comparative anatomy, because this indicates the tissue-creating potential of each organism which determines its possibilities for progressive mutations. These same considerations prevent the acceptance of Berrill's (1955) theory of descent from the ascidian tadpole.

From the data of comparative anatomy and paleontology, more conclusive evidence is to be found of a nautiloid-verte-

brate linkage. Although the possibility must be recognized that anatomy of the modern nautiloid, the pearly *Nautilus*, may differ in details from the Cambrian and Ordovician orders, it would seem safe to assume that the major anatomical features have remained the same. The modern *Nautilus* possesses the distinctive cardiovascular-respiratory-renal relationships found universally amid the vertebrates. This consists of a closed circulatory system in which *both* respiration and renal excretion are accomplished through the circulatory system, as compared, for example, with the open circulatory system of the arthropods wherein renal excretion and/or respiration are independent systems. Only amid the molluscs and the vertebrates is such a constant pattern seen. This should be contrasted with the complete lack of such developments in the echinoderm, which has no blood vascular system (Parker & Haswell, 1940).

Two apparently peculiar features of lower chordates become understood if the nautiloid ancestry is correct. The first is the presence of flame cells in the excretory system of *Amphioxus*— a type of cell found only in molluscs and lower forms. The second is the drainage of the pericardium by renal tissue, found both in cyclostomes and in cephalopods. These would seem to be residuals of early form relationships preserved in the chordates and pointing to a cephalopod ancestry, just as the gill slits of the mammalian embryo demonstrate their fish ancestry.

The profound importance of a highly-efficient cardiovascular, respiratory, and renal system in effectively oxygenating the blood and removing carbon dioxide and nitrogenous waste can hardly be over-estimated. For it is on the basis of an efficient method for bathing the tissues with the necessary substances and removing noxious wastes that the higher tissue and organ integrations characteristic of the vertebrates may be achieved. These basic and vital functions, upon which all further developments are based both embryologically and phylogenetically, are not likely to have been suddenly created in an echinoderm which shows no trace of such crucial functions. It takes specific genes to create such a system in the organism. Neither the echinoderm nor the arthropod has the genetic equipment to achieve this. Only the mollusc has.

One major universal feature of the vertebrates is the lens eye. From the lowest to the highest members of this subphylum, the eye appears at the onset in a perfected form and undergoes no radical subsequent transformation except in the cases of secondary degeneration. This organ would seem to have emerged "full grown from the brow of Zeus," as stated by Hagedoorn (1936) in apparent contradiction to the general rule in evolution of gradual development as seen for example in the vertebrate ear. Here again, a nautiloid ancestry could account for this apparent anomaly, inasmuch as gastropods, bivalves, and higher cephalopods all have developed lens eyes. This suggests that the eye of *Nautilus* may have degenerated from a more highly developed eye in the ancient orders.

The striking parallels between the vertebrate eye and that of the modern higher descendants of the nautiloids, the Sepioidea and the Octopoda, give further confirmation of a linkage between the cephalopods and the vertebrates. Except for the differences in embryonic origins and the positions of the retinal layers, the eyes of both vertebrates and higher cephalopods seem more nearly homologous than analogous structures. Both have an active iris, accommodating lens, cornea, sclera, rods, etc. (Prince, 1956). Analogous structures, such as insect, bird, and bat wings or insect and vertebrate auditory apparatus, accomplish their functionally similar ends with morphologically different structures. Both the vertebrate and the higher cephalopod accomplish their feat of vision with an organ which has the same gross and microscopic structures, thus strongly suggesting a common origin.

In this connection, it is to be noted that the central nervous system of *Sepia* (Ariens Kappers, 1929) more closely resembles the vertebrate brain than does that of any other invertebrate, having a three-part organization which brings to mind the embryonic vertebrate's prosencephalon, mesencephalon, and rhombencephalon. The higher cephalopods are "active, alert, and aggressive" (Schuchert & Dunbar, 1941), and have good vision. In these general behavior characteristics they again resemble

the vertebrates. These contrast strongly with the low level of perceptual, neural, and muscular development found amid the echinoderms.

Although in later stages of evolution, the vertebrates are distinguished by their universal endoskeleton, from which their name derives, the first vertebrates possessed an exoskeleton more conspicuous than the endoskeleton. Many of the first vertebrate endoskeletons were cartilagenous, like that of the cephalopod. In *Nautilus* the cartilage supports the brain ganglia, whereas in *Sepia* cartilage completely invests the ganglionic nerve collar so that emerging nerves pass through foramina as in vertebrates (Cunningham, 1910). Although a few arthropods also possess a cartilagenous endoskeleton, the exoskeleton is primarily chitinous. The echinoderms have no endoskeleton, only a calcareous exoskeleton. Only the cephalopods possess both a cartilagenous endoskeleton and a calcareous exoskeleton like those of the early vertebrates, offering another very basic resemblance between these two forms of life.

The earliest nautiloid cephalopod known is an orthocone or straight form (Twenhofel & Shrock, 1935). Many early cephalopods possessed, instead of a broad, open, circular external aperture like that in *Nautilus*, a constricted aperture which would resemble the mouths of such jawless, filter-feeding forms as *Kiaeraspis*, *Drepanaspis*, and *Pteraspis* (Romer, 1945, illustrations p. 27, 31, 32). Many of the first vertebrates had a relatively enlarged head area. If it were assumed that the posterior septal margins became flexible and the rear septa permeated with a musculature, an orthocone nautiloid with a constricted aperture is not very far removed from *Poraspis* with its segmental or quasi-septate external body structure (Romer, 1945, p. 31). The preservation of communication from the living chamber, which contains the body of the *Nautilus*, with the posterior septa through the siphuncle suggests the possibility that in earlier forms the animal extended rearward. It is also possible that the siphuncle constitutes the invertebrate antecedent of the vertebrate notochord.

In this connection, Twenhofel & Shrock (1935, p. 378) state "In life the siphuncle is occupied by a fleshy tubular prolongation of the visceral region known as the *siphon*. This fleshy tube is thought by some to represent a remnant from the early developmental stages of nautiloid evolution before the septa were full developed and when the visceral cone of the animal was much larger."

That the above theory of vertebrate origin may not be as fantastic as it would first seem is suggested by a homologous, or perhaps even analogous, process in the subsequent fin and extremity formation of higher vertebrates. For in them the musculature extended itself perpendicularly from the axis of the organism to grant the fish and the tetrapod, organs of propulsion. If such a lateral extension could be achieved in subsequent evolutionary advance, there is no *a priori* reason why a posterior extension might not have been the mechanism whereby a modified early nautiloid cephalopod became transformed into a primitive armored vertebrate.

The development of a constricted aperture may have been mechanically related to the posterior extension or internalization of the natutiloid's tentacles and its musculature. For with an incapacity to achieve motion through the forward opening, the only possibility would be through investing the rear septa and moving them through a squirming motion. This could have been achieved through a genetic duplication as seen in allele formation in which the anterior tentacles became duplicated by a series of modified posterior ones. Because of the close linkage of vision with motility such a doubling—similar to that hypothecated for the genesis of man (Sillman, 1955)—could have included the eye genes to create the second pair of eyes of the lower vertebrates (Edinger, 1956), the pineal eyes appropriately directed toward the posterior of the organism.

From this reconstruction, the forward tentacles would in time have been suppressed in favor of a rearward development. Such a suppressed set of genetic mutations could well have been the basis for the subsequent development of the jaw (a kind of extremity) as well as, in later evolution, the fins of the fish and the extremities of the tetrapod. In this connection the ten upper extremity digits of the tetrapod—a universal pattern in the vertebrate from am-

phibian to man, used largely to move the organism and draw food to the mouth—seem to resemble in more that a fortuitous manner the design of the squid with its ten tentacles doing the same thing in a different way.

From the above considerations, the hemichordata, cephalochordata, and the urochordata must be considered to be degenerate vertebrates rather than transition stages between invertebrates and vertebrates as implied by the Garstang theory and also developed by Berrill (1955). The meagre sensory and neural equipment of all these forms in a phylum characterized by a high and constant development of these structures suggests involution. The complete loss of sensation and motility by the adult tunicate as compared with its tadpole, its hermaphrodism and growth by budding, all point to a profound regression back to lower invertebrate functioning. For aside from the notochord, the lower chordates seem in many ways more primitive than the higher invertebrates, thus providing an instance wherein a vast and profoundly significant forward movement in evolution was accompanied by a marked regression in some offshoots.

On the basis of the material presented, it can be seen that the nautiloid cephalopod shares more cardinal features with the vertebrate than does the echinoderm. Embryologically there would seem to be a somewhat closer resemblance between the cephalopod and the vertebrate than between the latter and the echinoderm. In regard to the basic structuring of the circulatory, respiratory, renal, and skeletal systems *Nautilus* shows such marked similarities with the vertebrate that it almost seems justified to put them in the same class of animals. By contrast, the various echinoderms completely lack any distinctive basic adult vertebrate features. Further, the transformation of a nautiloid into a vertebrate can be constructed which violates no known evolutionary process, has the relative simplicity of commonplace morphological changes in evolution, and explains the puzzling feature of the vertebrate's pineal eyes.

In addition, the higher cephalopod descendants of the early nautiloids, the Sepioidea and the Octopoda, show in the gross and microscopic anatomy of the eye, the basic pattern of the brain, and the general behavior of the organism a marked resemblance to the vertebrate, pointing to a common ancestry.

Thus primarily from the evidence of comparative anatomy, secondarily from the data of comparative embryology, and thirdly from striking resemblances of a separate line of descent, the hypothesis is presented that the vertebrate originated from an orthoconic, nautiloid cephalopod.

BIBLIOGRAPHY

ARIENS KAPPERS, C. U., 1929, The evolution of the nervous system in invertebrates, vertebrates and man: Haarlem, De Erven F. Bohn.

DE BEER, G. R., 1951, Embryos and ancestors: x+108 p., 2 pls., Oxford, Clarendon Press.

BERRILL, N. J., 1955, The origin of vertebrates: 257 p., illus., Oxford, Clarendon Press.

BOLK, L., 1926, Das Problem des Menschwerdung: Jena.

CUNNINGHAM, J. T., 1910, Cephalopods: Encycl. Britt., 11th Ed.

EDINGER, T., 1956, Paired pineal organs: Progress in Neurobiology, 1956, p. 121.

FELL, H. B., 1948, Echinoderm embryology and the origin of chordates: Biol. Rev., v. 23, p. 81.

GARSTANG, W., 1894, Preliminary note on a new theory of the phylogeny of chordates: Zool. Anz., v. 444, no. 17, p. 119, 122–125.

GASKELL, W. H., 1908, The origin of vertebrates: London, Longmans, Green & Co.

HAGEDOORN, A., 1936, The comparative anatomy of the eye: Arch. Ophth., v. 16, p. 783.

MACBRIDE, E. W., 1914, Textbook of embryology, Volume I, Invertebrata: London, Macmillan.

PARKER, T. J., & HASWELL, W. A., 1940, A Textbook of Zoology, volume 1: xxxii+770 p., London, Macmillan.

PATTEN, W., 1912, The evolution of vertebrates and their kin: xxi+486 p., 309 figs., Phila., P. Blackiston's Son & Co.

PRINCE, J. H., 1956, Comparative anatomy of the eye: Springfield, Ill., Thomas.

RICHARDS, A., 1931, Outline of comparative embryology: p. xvi–444, 8 Vo., N. Y., J. Wiley.

ROMER, A. S., 1941, Man and the vertebrates: Univ. Chicago Press.

—— 1945, Vertebrate paleontology, 2nd ed.: Univ. Chicago Press.

—— 1949, The vertebrate body: p. 643, 363 illus., Phila.

SCHUCHERT, C., & DUNBAR, C. O., 1941, Outlines of historical geology: N. Y., Wiley.

SILLMAN, L. R., 1955, The genesis of man: Evolution, v. 9, no. 1, p. 94–99.

TWENHOFEL, W. H., & SHROCK, R. R., 1935, Invertebrate paleontology: xiv+511 p., illus., N. Y., McGraw-Hill.

YOUNG, J. Z., 1950, The life of vertebrates: xvi+767 p., 497 figs., Oxford, Clarendon Press.

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A TERTIARY *CYNOMYS* FROM SOUTH DAKOTA

MORTON GREEN
Museum of Geology, South Dakota School of Mines and Technology, Rapid City, South Dakota

ABSTRACT—A new species of Tertiary prairie dog, *Cynomys spispiza*, is represented by a partial lower jaw that was found on the surface of a Valentine sand. The species is compared with *Cynomys ludovicianus* and *C. leucurus* to which the fossil is related. The temporal range of the genus is extended to the early Pliocene or late Miocene. No evidence is available to determine the ancestry of *Cynomys*.

INTRODUCTION

WHILE making reconnaissance and mapping Tertiary deposits in Tripp, Gregory, and Charles Mix Counties, the South Dakota State Geological Survey collected some fossil vertebrates. Among these was a sciurid lower jaw collected by Dr. R. E. Stevenson from the surface of a Valentine sand. The specimen has been turned over to the Museum of Geology for cataloguing and storage.

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Family SCIURIDAE

CYNOMYS SPISPIZA* n. sp. Green

Type.—SDSM No. 57100; fragment of left lower jaw bearing P_4-M_3.

Type locality.—$NE\frac{1}{4}$, $NE\frac{1}{4}$, $SE\frac{1}{4}$ sec. 20, T. 97 N., R. 74 E., spillway of Roosevelt Lake dam, Tripp County, South Dakota.

Fauna and Age.—Valentine. Late Miocene or early Pliocene.

Diagnosis.—P_4 relatively larger than in Recent species. Mid-line of protolophid in M_{1-3} opposite ectolophid of preceding tooth.

Description.—P_4: Crown of protoconid worn slightly, enamel merging with metalophid and ectolophid; small notch in enamel of posterior border of protolophid valley, parametaconid worn; small cuspid labiad of parametaconid (possibly protoconulid); hypoconid thin; folded enamel of talonid basin barely discernible; posterior border of posterolophid with small tubercles. M_1: Protolophid and metalophid united by wear; lingual side of hypoconid rounded; prominent enamel protuberance linguad of parametaconid; mid-line of protolophid opposite ectolophid of P_4; hypoconid and entoconid connected by worn posterolophid; enamel of talonid basin gently folded. M_2: Much like M_1; enamel crest linguad of broken parametaconid longer than in M_1 and connected to parametaconid. M_3: Enamel crest linguad of broken parametaconid, terminating in a small dentine ridge directed lingually; small basal cuspid at base of hypoflexid.

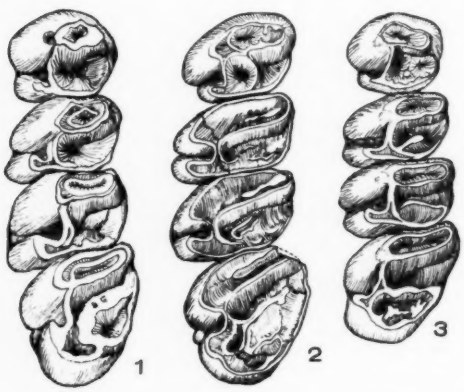
Comparison and relationship.—The dental series is about the same length as in *Cynomys ludovicianus* (Ord) and longer than in *C. leucurus* Merriam. P_4 in *C. ludovicianus*, though a parallelogram in outline, is nearly quadrate. In *C. spispiza* and *C. leucurus* the outline is more nearly a parallelogram, particularly in a worn tooth. The small tubercles on the posterior edge of the posterolophid are developed to an identical degree in *C. spispiza* and *C. leucurus*. This character is much less developed in *C. ludovicianus* if at all. In M_1 and M_2 of *C. ludovicianus* the anteriorly projecting bulge in the center of the protolophid is decidedly more prominent than in the other two species. It is this bulge which give the teeth a nearly quadrate outline. The enamel ridge which is all that remains of the valley between the parametaconid and protoconid is most prominent in *C. spispiza*. In M_3 there is a

* Sioux Indian (Teton Dakota) for prairie dog. Name supplied by Frank C. Estes of Lower Brule Reservation.

TABLE 1—MEASUREMENTS IN MILLIMETERS

	C. spispiza SDSM No. 57100	*C. leucurus* CUM No. 128	*C. ludovicianus* CUM No. 3176
P_4 A-P	3.0	2.5	3.0
P_4 Tr	4.5	3.7	4.3
M_1 A-P	2.9	2.4	3.3
M_1 Tr	4.7	3.4	4.0
M_2 Tr	3.0	2.5	3.0
M_3 A-P	4.9	4.7	5.7
M_3 Tr	4.2	3.6	4.0
P_4-M_3	15.2	13.0	15.4

cuspid at the base of the hypoflexid in both *C. leucurus* and *C. spispiza*. This cuspid is *absent* in *C. ludovicianus*. Bryant's (1945, pl. 4, fig. b) figure of *C. gunnisoni* (Baird) also displays this cuspid. In all of the teeth the hypoconids are relatively larger in *C. spispiza* and *C. ludovicianus* than in *C. leucurus*. In *C. spispiza* and *C. leucurus* the hypoconids turn anteriorly but slightly. In *C. ludovicianus* they are sharply bent toward the protoconid. Consequently, the protoconids and hypoconids are farther apart in the former species. *C. spispiza* differs from the other two species in that the mid-point of the protolophid of M_{1-3} are opposite the ectolophid of the preceding tooth. In the two Recent species, the center of the protolophid is linguad of the ectolophid.



TEXT-FIG. *1. Cynomys ludovicianus;* CUM No. 3176, from near Boulder, Colorado. Crown view, left P_4-M_3, ×4.

TEXT-FIG. *2. Cynomys spispiza* n. sp. Green; SDSM No. 57100. Crown view, left P_4-M_3, ×4.

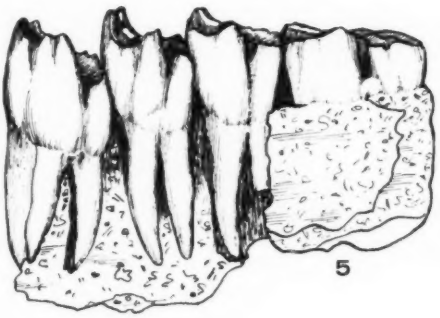
TEXT-FIG. *3. Cynomys leucurus;* CUM No. 128, from near Meeker, Colorado. Crown view, left P_4-M_3, ×4.

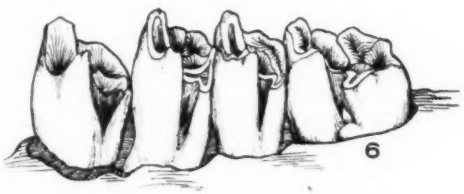
C. spispiza combines characteristics of both *C. ludovicianus* and *C. leucurus* but is closer to the latter species. Whether or not *C. spispiza* is ancestral to these species (and other Recent species of the genus) is difficult to determine on the evidence provided by the single specimen. The fossil species and *C. ludovicianus* are similar in size, the hypoconids are relatively large, and M_3 is broad across the protolophid and metalophid. The resemblance of *C. leucurus* to *C. spispiza* is in the general outline of the teeth, similarly shaped hypoconids, the presence of the basal cuspid in M_3, and in the cuspidate posterolophid of P_4. Superficially at least, it seems as though *C. spispiza* could be ancestral to both these Recent species and it is not illogical to provisionally consider it to be the ancestor.

Some comment as to the evolutionary position of *Cynomys* is necessary. Bryant (1945) concluded that *Cynomys* and *Citellus* (*Citellus*) are either closely related or convergent genera. His preference was that they are closely related because the subgenus *Citellus* resembles *Cynomys* in skull structure and dentition more than it does the other subgenera of *Citellus*. His phylogenetic chart indicates that *Cynomys* is an offshoot of *Citellus* possibly in mid-Pliocene time.

It is necessary to alter Bryant's conclusions which were made without the new material discussed here. Since the age of the new species cannot be more precisely stated than either late Miocene or early Pliocene, I am arbitrarily assuming it to be of early Pliocene age. This would conservatively extend the temporal range of the genus from early Pliocene time to Recent. Even if we assume that *Cynomys* is derived from *Citellus* the phylogenetic chart should be modified in extending the *Cynomys* line back to near the base of the Pliocene, at least.

There is apparently no relationship between *C. spispiza* and such forms as *Protospermophilus* Gazin (Upper Miocene and Lower Pliocene) and *Citellus primitivus* Bryant (Upper Miocene). There also seems to be no more reason to consider the resem-





TEXT-FIG. *4. Cynomys ludovicianus;* CUM No. 3176. Labial view, P_4-M_3, ×4.
TEXT-FIG. *5. Cynomys spispiza* n. sp. Green; SDSM No. 57100. Labial view, P_4-M_3, ×4.
TEXT-FIG. *6. Cynomys leucurus;* CUM No. 128. Labial view, P_4-M_3, ×4.

blance of *Cynomys* to *Citellus* as one of close relationship than as the result of convergence. The ancestry of *Cynomys* is as yet unknown.

Faunal relationship.—To the best of my knowledge, *C. spispiza* represents the first known occurrence in South Dakota of a fossil vertebrate from beds equivalent in age to those in Cherry County, Nebraska. A possible exception to this might be those vertebrates from the Bijou Hills area in Brule County, South Dakota known as the Bijou Hills local fauna (Wood, H. E., 1941). This fauna is considered to be late Miocene in age, particularly because of the presence of *Merychippus insignis* Leidy, *Leptarctus primus* Leidy, *Gomphotherium fricki* Peterson and *Merycodus necatus* Leidy (Green, 1958). At the present time, the relationship of the Bijou Hills sediments to lithologically similar beds to the south is in dispute (Agnew, 1958; Green, 1958; Stevenson, 1958). Unfortunately, this sciurid does not help us in resolving the Bijou Hills problem.

Stevenson (pers. comm.) states that the specimen was found in a buff colored fine grained arkose sand about 20 feet above the Pierre shale contact and about 10 feet below the Bijou formation. Stevenson's (1958) remarks on the Bijou formation do little to clarify either the stratigraphic or nomenclatural status of the name (Bijou). Rather there seems to be an effort to preserve a formational name that never should have been proposed. I would also suggest, and J. R. Macdonald (pers. comm.) agrees, that to give the various "green quartzose" beds in the Bijou Hills one name would be the same as giving the different channels of the White River Group a separate formational name. That this is precisely what Stevenson has in effect done is evidenced by Taft's (1959) interpretation of Stevenson in which he states that the Ogallala Group "consists of the Ash Hollow (formation) conformably over-lying the Valentine formation, with the Bijou formation found within each."

REFERENCES

AGNEW, A. F. 1958. Bijou formation—a stream deposit? Proc. S. Dak. Acad. Sci., v. 36, p. 129–133, 1 fig.

BRYANT, M. D. 1945. Phylogeny of Nearctic Sciuridae. Amer. Mid. Nat., v. 33, no. 2, p. 257–390, 48 figs., 8 pls.

GREEN, M. 1958. *Gomphotherium fricki* from the Bijou Hills, South Dakota. Proc. S. Dak. Acad. Sci., v. 36, p. 139–142, 2 figs.

STEVENSON, R. E. 1958. Revision and interpretation of the Bijou formation. Proc. S. Dak. Acad. Sci., v. 36, p. 134–138, 1 fig.

TAFT, W. H. 1959. The Ogallala group of south-central South Dakota. Proc. S. Dak. Acad. Sci., v. 37, p. 146–147.

WOOD, H. E.; 2nd, *et al.* 1941. Nomenclature and correlation of the North American Tertiary. Bull. Geol. Soc. Amer., v. 52, p. 1–48, 1 pl.

MANUSCRIPT RECEIVED MAY 2, 1959

JOURNAL OF PALEONTOLOGY, V. 34, NO. 3, P. 548–550, 2 TEXT-FIGS., MAY, 1960

BISON LATIFRONS IN SOUTH DAKOTA

MORTON GREEN AND HAROLD MARTIN
Museum of Geology, South Dakota School of Mines and Technology, Rapid City, South Dakota

ABSTRACT—A nearly complete skull with horn cores of *Bison latifrons* (Harlan) is average in size for the species and marks the most northern find to date. The stratigraphic range of the species is either Medial to Late Pleistocene or Late Pleistocene only.

INTRODUCTION

DURING the summer of 1958, the director of the Museum of Geology, J. D. Bump, received a letter from E. L. Tuning stating that a large skull had been uncovered during quarry operation in a sand and gravel deposit near Midland, South Dakota. The senior author contacted Mr. Tuning and learned that the skull had been removed from the site in pieces. The many fragments were donated to the museum. Missing was one horn and many smaller fragments.

At a later date, it was learned that the missing horn was in the possession of Lester D. Hilson, also of Midland. This horn plus a few skull fragments were obtained from Hilson by Ralph Jones of Midland who is owner of the quarry. It is fortunate that Mr. Jones is not only the owner of the property and felt that we should have the missing horn, but he is also the South Dakota School of Mines and Technology representative on the State Board of Regents and, as a regent, wished to secure the specimen for scientific study. We are particularly indebted to Mr. Jones and all people concerned in seeing to it that the specimen did not end up as a curiosity on someone's mantelpiece.

SYSTEMATIC DESCRIPTION

BISON LATIFRONS (Harlan)

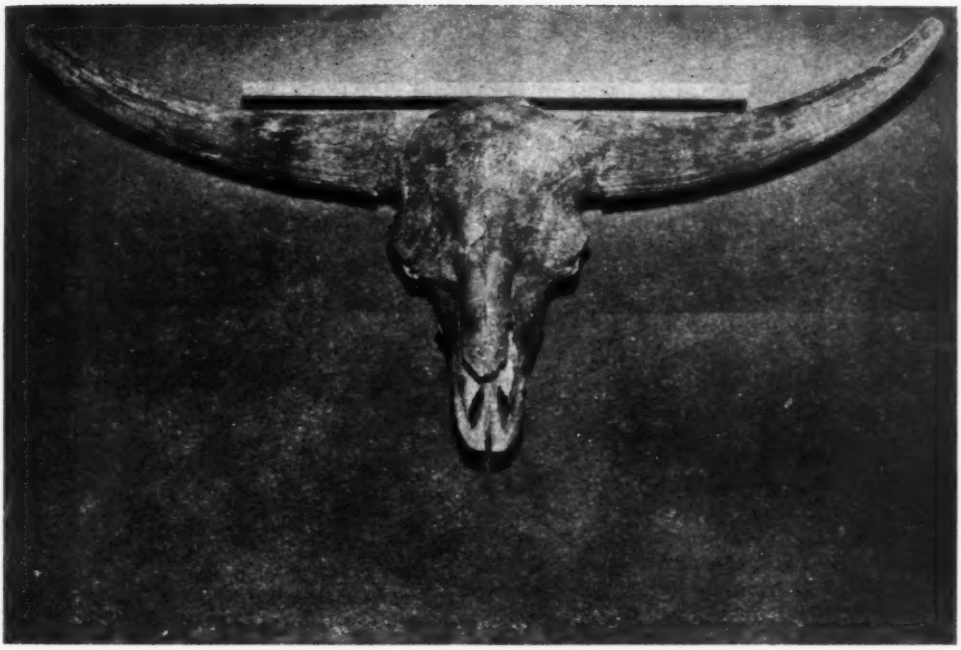
Referred specimen: SDSM No. 5889; most of skull with left P^4-M^3, right P^3-M^3, and horn cores present, with the tip of the left horn, tips of the maxillae, portions of the palate, and the pterygoid processes missing. Locality: SW¼, SW¼, Sec. 31, T. 2 N., R. 25 E., Midland Quadrangle, Haakon County, South Dakota. This is about 1.2 miles north of the town of Midland just north of the Bad River.

This specimen represents the 22nd record

TABLE 1—MEASUREMENTS IN MILLIMETERS

	Left	Right
Core length on upper curve, tip to burr	743	812
Length of core on lower curve, tip to burr	787	855
Length, tip of core to upper base at burr	717	796
Transverse diameter of core	161	167
Vertical diameter of core	136	138
Circumference of core at base	484	494
P^3 A-P		22.8
P^3 Tr		21.7
P^4 A-P	20.0	21.5
P^4 Tr	25.4	25.4
M^1 A-P	25.5	25.6
M^1 Tr	30.0	29.4
M^2 A-P	33.3	34.8
M^2 Tr	32.3	31.7
M^3 A-P	36.6	35.8
M^3 Tr	31.6	31.6
Length M^{1-3}	96.8	97.0
P^2-M^3 alveolar length	165.0	170.0
Spread of horn-cores, tip to tip		1726*
Greatest spread of cores on outside curve		1778*
Width cranium between cores and orbit		355
Greatest postorbital width		395
Width of skull at masseteric processes at M^1		219
Greatest width at auditory openings		340
Width of condyles		157
Occipital crest to nasal-frontal suture		310
Occipital crest to lower border foramen magnum		181
Basilar length of skull		609*
Over-all length of skull		681*
Median length of premaxilla beyond P^2		153*
Rostral width at maxillary-premaxillary suture		151
Length, occipital crest to tip of nasals		554
Length of nasal bone		254
Anterior orbital width at notch		282
Width between bases of horn-cores		310
Index of horn curvature		107
Index of core compression		83
Index of core proportion		165
Index of core length		229
P^2-M^3/skull length; in percent		27
Distance between anterior premolars		95*
Distance between posterior molars		120

* Approximate.



TEXT-FIG. *1*—*Bison latifrons* (Harlan) referred, SDSM No. 5889, as seen from above. Length indicated by meter stick. Photo by Richard Kitchen.

TEXT-FIG. *2*—View of gravel pit showing cross-bedding. Hammer at probable level of skull. Photo by Richard Kitchen.

of the species, and the first record of the species in South Dakota. As far as can be determined, it is the most northern find for the species as well (see Skinner and Kaisen, 1947, p. 154). From the accompanying measurements, it can be seen that in most instances the South Dakota specimen falls in the average or slightly less than the average in size for the species as given by Skinner and Kaisen (p. 205, 207).

The stratigraphic range of *B. latifrons* has been in doubt. Schultz and Frankforter (1946) believed that this giant bison arrived in the Great Plains during Kansan time (early Medial Pleistocene). The same authors (1951) tentatively refer the species to a Kansan or Yarmouth Age. Skinner and Kaisen (1947 p. 155) mention that the species may have survived until Late Pleistocene in Florida. This is probably the specimen from the Bradenton quarry described by Simpson (1930). Savage (1951) reports a specimen from a soil layer near Walnut Creek, California, giving for the age of the deposit later Pleistocene. However, no definitive age for the specimen was given. VanderHoof (1942) gives for the very fine University of California skull an age of Late Pleistocene.

According to Flint (1955) the probable age of the terraces north of the Bad River is Late Pleistocene. As worked out by Crandell (1954) these terraces range in age from early to late Pleistocene. The SDSM specimen comes from the highest of several terraces in the area and the oldest possible dating is Iowan. The deposit consists of fine to coarse cross-bedded sands with pebbles up to at least one inch in diameter.

Possibilities remaining then, in the interpretation of the species relative to the stratigraphic level(s) in which it is found, are: (1) *Bison latifrons* survived into the Late Pleistocene in all, or nearly all, of its geographic range. (2) The interpretations of Schultz, *et al.* and Skinner and Kaisen are not valid, and *B. latifrons* is found only in deposits of Late Pleistocene Age.

REFERENCES

CRANDELL, D. R., 1954, Geology of the Pierre Quadrangle (1:62500). U. S. Geol. Surv., Dept. of the Interior, Wash., D. C.

FLINT, R. F., 1955, Pleistocene Geology of Eastern South Dakota. U. S. Geol. Surv., Prof. Pap. 262, vi+173, 36 figs., 7 pls.

SAVAGE, D. E., 1951, Late Cenozoic vertebrates of the San Francisco Bay Region. Univ. Calif. Publ., Bull. Dept. Geol. Sci., Vol. 28, No. 10. 215–314, 51 figs.

SCHULTZ, C. B. & W. N. FRANKFORTER, 1946, The geologic history of the bison in the Great Plains (a preliminary report). Bull. Univ. Neb. State Mus., Vol. 3, No. 1, 1–10, 1 fig.

——, 1951, In: SCHULTZ, C. B., G. C. LUENINGHOENER, & W. D. FRANKFORTER. A graphic resume of the Pleistocene in Nebraska. Bull. Univ. Neb. State Mus., Vol. 3, No. 6, 1–41.

SIMPSON, G. G., 1930, Additions to the Pleistocene of Florida. Amer. Mus. Novit. No. 406, 1–14, 7 figs.

SKINNER, M. F. & O. C. KAISEN, 1947, The fossil *Bison* of Alaska and preliminary revision of the genus. Bull. Amer. Mus. Nat. Hist., Vol. 89, Art. 3, 123–156, 5 figs., 19 pls.

VANDERHOOF, V. L., 1942, A skull of *Bison latifrons* from the Pleistocene of Northern California. Univ. Calif. Publ., Bull. Dept. Geol. Sci., Vol. 27, 1–24, 5 figs., 2 pls.

JOURNAL OF PALEONTOLOGY, V. 34, NO. 3, P. 551–555, 3 TEXT-FIGS., MAY, 1960

A TRILOPHOSAURID REPTILE FROM THE KOOTENAI FORMATION (LOWER CRETACEOUS)

EVERETT C. OLSON
University of Chicago

ABSTRACT—A new genus and species of reptile of the Family Trilophosauridae is described. The specimen upon which the description is based was found in the Kootenai Formation, Lower Cretaceous, of Montana. Previously the family has been known only from the Upper Triassic.

INTRODUCTION

IN THE course of mapping, while carrying out class work at the Montana School of Mines, Mr. George Cloud of Juneau, Alaska, found a pair of small jaws in the Kootenai formation of Montana. The specimen was encased in red silt-stone and its affinities among the vertebrates were not at once evident. The specimen was sent to the writer for identification by Dr. O. D. Blake, now Geologist of the Oil and Gas Conservation Commission of the State of Montana. It proved to be of considerable interest and with the donor's permission it has been deposited in the collections of the Chicago Natural History Museum, C.N.H.M. UR 619. Subsequently, Dr. Blake furnished precise geological and locality data, which have been incorporated in this report. I wish to express my sincere appreciation to Dr. Blake for sending the specimen, for permission to publish upon it, and for the indispensable information upon the location and geological situation in which it was found.

SYSTEMATIC DESCRIPTION

ORDER PROTOROSAURIA
Family TRILOPHOSAURIDAE
Genus TOXOLOPHOSAURUS n. gen.

Diagnosis.—Lower jaw with 20 or 21 cheek teeth, lacking teeth in symphysial region. Teeth progressively larger from anterior to posterior along the jaw. Each tooth with sharp, transverse crest, curved anteriorly on lingual margin. Inner margin of each tooth sharply inflected anteriorly to overlap inner margin of next anterior tooth. Labial surface of crown roughly triangular.

Symphysis of jaw deep, rather narrow, and sloping postero-ventrally to produce a symphysial shelf. Adductor fossa short, sloping posteroventrally and encased laterally and medially by prearticular bone. Open Meckelian groove on inner margin of jaw from level of coronoid process to symphysis. Coronoid process strong, formed by large coronoid bone and by the dentary bone.

TOXOLOPHOSAURUS CLOUDI n. sp.

Holotype.—C.N.H.M. UR 619. Pair of lower jaws lacking articular area on both sides.

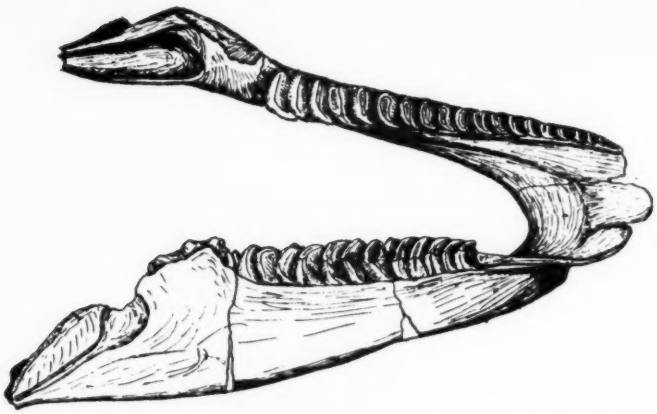
Horizon and locality.—Kootenai formation, lower Cretaceous. 223.75 feet above base of Kootenai. T. 4 S., R. 8 W., W. Cent. NE SE Sec. 23, Silver Bow County, Montana. Aerial photo index (see Olson, 1948), CXK 3B 25, 4.31–5.94 (1942 Photo. series).

Diagnosis.—Same as for genus.

Description.—Preservation of the specimen is in general good. By use of the features on the two jaws, it has been possible to interpret most of the essential features. The nature of the specimen, its degree of completeness, and the amount of distortion are shown in text-figure 1. It will be noted that the anterior teeth are highly worn and that there is successively less wear posteriorly with the final tooth on each side virtually unworn.

The major features of the jaws are noted in the diagnosis and illustrated in text-figures 1,2, and 3. Certain of these require special emphasis because of their taxonomic significance.

The dentary is proportionately large and well developed along the inner, ventral margin of the jaw. It extends posteriorly in a short spur below the coronoid process, on the outer surface of the jaw, to wedge between the angular below and surangular



TEXT-FIG. *1*—Drawing of lower jaws of *Toxolophosaurus cloudi* n. gen and sp. (holotype, CNHM UR 619), showing jaws as preserved in dorsal view. ×1½.

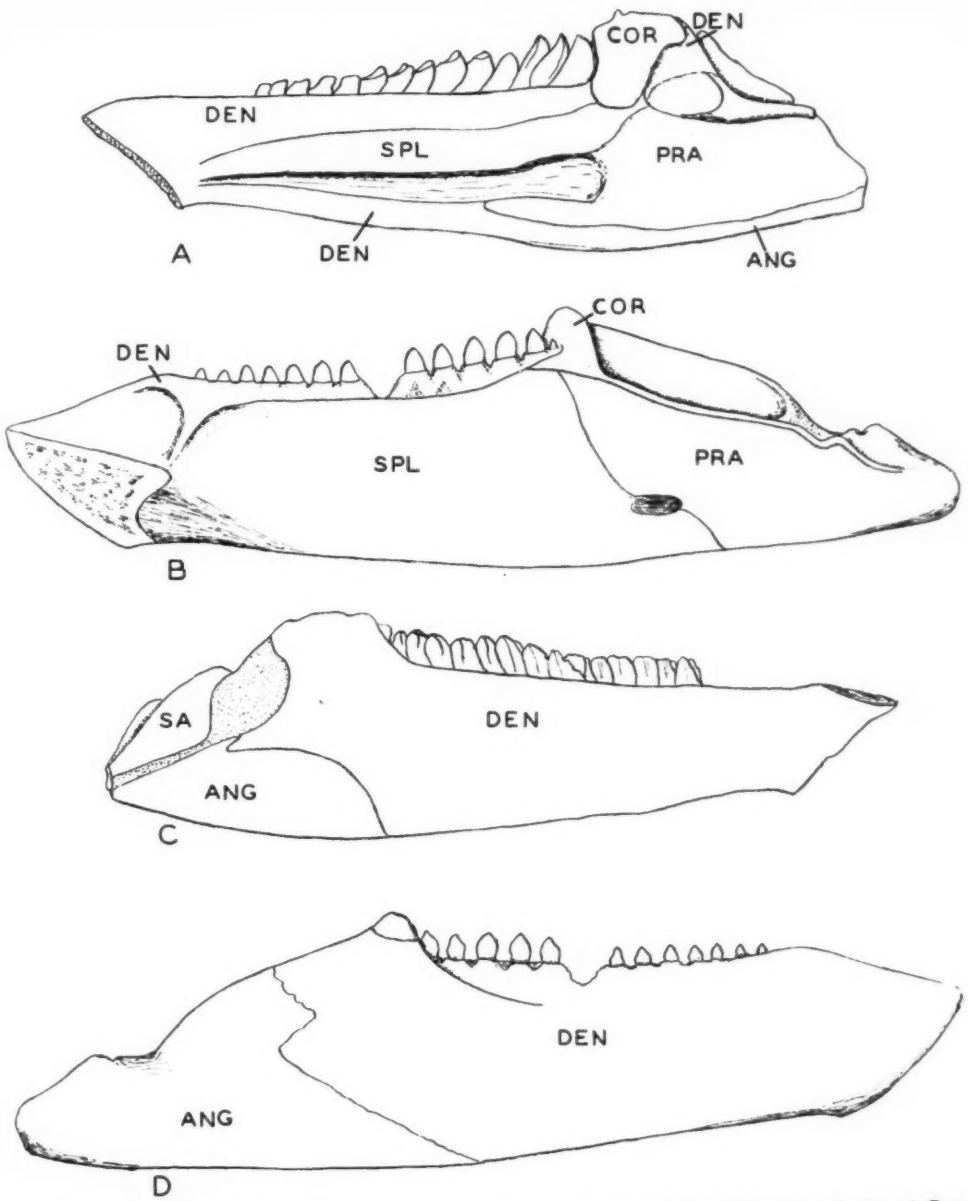
above. It rises to form the outer surface of the strong coronoid process to cover the coronoid bone laterally. Between the dentary and surangular there is a zone that lacks bone and in which part of the prearticular is visible in lateral aspect. This condition is clearly seen on the right half of the jaw, but is less clearly defined on the right. In this zone, in the adductor fossa, there appears to be an opening with regular margins between the prearticular and dentary, suggesting the existence of an actual fossa. It seems quite possible that there was, in fact, a fossa that passed to the outer surface of the jaw, but it may well be that the surangular, which is immediately adjacent, extended in a very thin sheet of bone over the open area; a sheet that was not preserved because of its extreme delicacy.

On the lingual surface of the jaw there is a well developed Meckelian groove. Its dorsal margin is formed by the splenial. The groove passes forward from the level of the anterior margin of the coronoid process to the symphysis. The splenial appears to be preserved in its entirety and apparently did not cover this groove as it does in many reptiles. Thus the splenial was a long, slender element on the inner surface of the jaw below the dentary and above the Meckelian fossa.

The coronoid process is a very prominent feature of the jaw. It is incomplete dorsally on both sides, but clearly rose well above all other structures of the jaw. The coronoid bone forms the process internally, but the outer portion is formed by the dentary. Back of this process is a short adductor fossa whose outer margin slopes sharply posteriorly toward the unpreserved articular portion of the jaw. The fossa lies almost wholly within the pre-articular bone, which is the dominant element of the posterior part of the jaw.

The main features of the dentition are shown in figures 1,2 and 3. The absence of anterior teeth is real, and not a matter of poor preservation. Apparently all the cheek teeth were characterized by a sharp crossloph that swung sharply forward along the inner margin of the tooth. Wear is heavy on the anterior teeth, but the successive stages of wear, decreasing posteriorly, suggest a common crown pattern along the whole series. On the unworn last teeth the crossloph is sharp and smooth and shows no evidence of cuspules. Dimensions of the teeth, expressed as maximum width, increase regularly front anterior to posterior as follows:

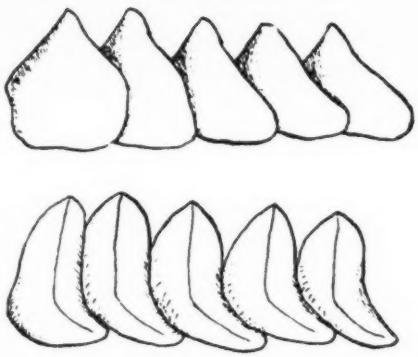
Tooth number	width in mm.
3rd	0.8
5th	1.3
10th	2.0
15th	3.0
20th	4.0



TEXT-FIG. 2.—Jaws of *Toxolophosaurus cloudi* n. gen. and sp. and *Trilophosaurus beuttneri* Case. Jaws to proportional scale. A. lingual view of *Toxolophosaurus cloudi;* B. lingual view of *Trilophosaurus beuttneri;* C. labial view of *Toxolophosaurus cloudi:* D. labial view of *Trilophosaurus beuttneri. Trilophosaurus* after Gregory (1945). Abbreviations: ANG., angular; COR., coronoid; DEN., dentary; PRA., prearticular; SA., surangular; SPL., splenial.

TABLE 1—SECTION OF KOOTENAI FORMATION AT SITE OF *Toxolophosaurus cloudi*, SUPPLIED BY DR. O. D. BLAKE. *BED IN WHICH SPECIMEN WAS FOUND

Colorado formation: Kootenai formation:	Feet
48. Limestone, vertically jointed, medium gray, with scattered fossil fragments	1.5
47. Limestone, massive evenly bedded, medium dark gray, with abundant gastropods	23.0
46. Limestone, massive, gastropod coquina	8.0
45. Limestone, splintery vertically jointed	1.0
44. Limestone, ribbon like beds, dirty medium dark gray, with many gastropod fragments	31.0
43. Limestone, massive, medium dark gray, with scattered gastropod fragments	4.0
42. Limestone, ribbon like bedding, finely crystalline, medium gray	8.5
41. Limestone, massive, dirty medium gray	6.0
40. Poorly exposed, some shows of pale red and yellowish green, calcareous claystone and siltstone and scattered small limestone nodules	275.0
39. Sandstone, massive, friable, crossbedded, fine texture, yellowish gray	50.0
38. Siltstone, chippy, calcareous, pale orange, poorly exposed	95.0
37. Limestone, massive splintery, medium gray to dark green	9.0
36. Mostly covered, some show of claystone, blocky, calcareous, light to medium gray	15.5
35. Limestone, finely crystalline, brownish gray, with gastropods	5.0
34. Mostly covered, some show of dolomite, medium light gray	31.0
33. Limestone, light gray, fine texture, with closely spaced vertical joints, in four beds each underlain by thin light gray clay	15.0
32. Mostly covered but with some shows of white to very light gray calcareous clay, medium gray limestone, and light brownish-green calcareous claystone	95.0
31. Sandstone, coarse to medium texture, light gray salt and pepper	1.5
30. Limestone conglomerate, fragments up to 1″, very light blue-gray	1.5
29. Covered, some show of light brownish-gray calcareous, blocky claystone and small calcareous nodules	25.5
28. Sandstone, light gray, salt and pepper, medium textured, friable	5.0
27. Limestone conglomerate, with fragments up to 2″, medium light gray	1.5
26. Very poor exposure, some show of light brownish-gray calcareous claystone	16.5
25. Nodular limestone, medium light gray, fine texture	3.0
24. Claystone, blocky, grayish-red, pale red, and medium dark red, with some limestone nodules, poorly exposed	57.0
23. Sandstone, salt and pepper, medium light gray, calcareous, bottom very calcareous with irregular limestone granules	14.0
22. Siltstone, pale reddish to pale reddish-brown, calcareous	18.5
21. Sandstone, light olive gray, fine textured	3.5
20. Sandstone, massive, crossbedded, medium gray, salt and pepper, medium textured except for 1′ conglomerate at the base	24.0
19. Conglomerate with granules to 1″ of grayish-yellow, irregular shaped calcareous claystone in a matrix of coarse textured, salt and pepper sandstone	3.5
18. Claystone, calcareous, blocky, pale reddish-brown, poorly exposed	21.0
17. Sandstone, yellowish-gray, very fine textured calcareous	3.0
16. Sandstone, thin bedded, pale red, very fine grained, calcareous	31.0
15. Limestone granule conglomerate, massive, light gray, grayish-yellow and light red	3.0
14. Claystone, pale red, lumpy, calcareous, mottled	42.0
13. Sandstone, massive, pale red, fine textured, calcareous	1.0
12. Mostly covered, some shows of moderate orange pink, blocky, calcareous siltstone	6.0
11. Sandstone, thin bedded 1″ to 3″, slabby, light olive gray, medium texture, some stained pale red	29.0
*10. Siltstone, calcareous, splintery, calcareous, pale reddish-brown, gray, and orange pink. (Vertebrate fossil found 21″ below the top of this bed)	58.5
9. Sandstone, light brownish-gray, medium textured, calcareous, massive	2.0
8. Siltstone, blocky, calcareous, pale red, partly covered	13.5
7. Limestone, light olive gray, massive, fine texture	1.5
6. Claystone, blocky, gray red, poorly exposed; ⅔ of the way up from the base 1″ calcareous claystone nodules	46.5
5. Sandstone, massive, light brownish-gray, medium texture, crossbedded with thin limestone conglomerate and shale breaks near the top	10.0
4. Claystone, blocky, grayish red and pale olive, with scattered limestone nodules, poorly exposed	20.0
3. Sandstone, massive, pale yellow-brown, salt and pepper, coarse texture	3.5
2. Claystone, blocky black red, with small ½″ to 2″ limestone nodules	50.0
1. Sandstone, massive, salt and pepper, light yellow gray, coarse, lower part conglomeratic, with quartz pebbles ½″ to 3″	20.0
Total thickness of Kootenai formation	1210.0
Morrison formation:	



TEXT-FIG. 3—Sketch showing restoration to unworn condition of posterior teeth of *Toxolophosaurus cloudi* in labial and crown views.

Discussion

Occurrence.—The specimen was found in a red, calcareous siltstone in bed 10 of the section given in table 1. This bed appears to be of terrestrial origin, but little more can be said of conditions of deposition from the information available. Vertebrate remains are extremely rare in the Kootenai formation, being otherwise mostly unidentifiable scrap. Thus this new specimen may eventually take on considerable importance from a stratigraphic point of view. At present, however, nothing at all close to it has been found elsewhere in the Cretaceous and the interest is primarily biological. A very close search of the vicinity of the find was made, but no additional specimens could be located. The specimen, thus, becomes one of the rare bits of information pertaining to vertebrate life during Kootenai times.

Relationships.—The superficial appearance of the jaws of *Toxolophosaurus* is immediately reminiscent of *Trilophosaurus*, but the age difference, Early Cretaceous and Late Triassic respectively, is sufficient to make for caution in consideration of relationships. Careful study, however, appears to leave little doubt that the two genera are, in fact, closely related.

The cross-lophed teeth of the two represent a strong area of similarity, but in details the teeth are quite different. The forward swing of the loph along the inner margin in *Toxolophosaurus* is not found in *Trilophosaurus*, and the "cusp" pattern of the loph in *Trilophosaurus* is absent in *Toxolophosaurus*. In both genera there appears to have been no tooth replacement. Rather teeth erupted successively from anterior to posterior and were retained once they were present. This is an unusual pattern in reptiles and strongly suggests close relationship. The resemblance of the teeth give good evidence of relationship, but are not, of course, definitive. The absence of anterior teeth and the shelf-like symphysial region also represent features that are uncommon in reptiles, except among those possessing a pre-dentary element, and strongly support the dental evidence.

Comparisons of the jaw structure, the general form and details of the bones, show many striking resemblances between the two genera (see figure 2). The long dentary, the large pre-articular, the short sloping adductor fossa, the very low articular region, the strong coronoid process and the symphysial region produce a very comparable jaw structure. Each of these taken alone can be considered adaptive and it is, of course, possible that the total pattern may in itself represent a case of extremely strong convergence. It seems highly improbable, however, that the interrelated suites of jaw and dental characters would show the degree of similarity were there not an actual relationship at least at a familial level.

Assignment of *Toxolophosaurus* to the trilophodontidae extends the range of this family from the Upper Triassic to the Lower Cretaceous. No Jurassic representatives are known. This pattern of sporadic occurrence in the geological record is characteristic of the Protorosauria as a whole and has even cast considerable doubt upon its ordinal unity. Romer (1947) has argued convincingly for the homogeniety of the group. It may well be that the sparse record results from the environment in which these animals lived, one which was seldom tapped by processes that resulted in the fossil record.

REFERENCES

GREGORY, J., 1945, Osteology and Relationships of *Trilophosaurus*, Univ. Texas Publ., 4401, p. 273–359.

OLSON, E. C., 1948, A Preliminary Report on Vertebrates from the Permian Vale Formation of Texas, Jour. Geology, v. 56, p. 186–198.

ROMER, A. S., 1947, The Relationships of the Permian Reptile *Protorosaurus*, Am. Jour. Sci., v. 245, p. 19–30.

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VARIATION OF ENGLISH BATHONIAN LAGENIDAE AND ITS PHYLOGENETIC SIGNIFICANCE

RICHARD CIFELLI
U. S. National Museum, Washington, D. C.

ABSTRACT—Study of the English Bathonian emphasizes the need for recognition of variable species in the classification of the Jurassic Lagenidae. There is evidence that generally accepted generic as well as species characters vary considerably within a single species of this difficult group. It is suggested that "key" characters used to define genera should be treated cautiously and evaluated in light of other test features. Additional important clues in the taxonomy of this group are factors of distribution and the occurrence of transitional forms between distinct types in a single assemblage.

Recognition of variable species among the Jurassic Lagenidae is compatible with genetic and evolutionary theory. Moreover, the occurrence of variants is believed to provide important clues to the phylogeny of the group. The occurrence of identical structural types in distinct lineages suggests that many of the described genera of Lagenidae are polyphyletic.

INTRODUCTION

IN THE course of a study of English Bathonian Foraminifera (Cifelli, 1959) the writer became conscious of the bewildering variety of Jurassic Lagenidae and the difficulties of classifying them. Althought there have been many lagenid species and genera described from the Jurassic it soon became apparent that many of the English Bathonian forms did not correspond well with any of these taxa. The problem was not one of interpreting new structures, as the English Bathonian lagenids exhibit little new in morphology that has not already been described. The difficulty was in assessing the taxonomic significance of the wide variations that these structures exhibit and the numerous combinations in which they occur.

The highly variable nature of the Jurassic Lagenidae has been long known, although there have been but few attempts to investigate the possibility that much of the variation may be infra-specific (most notable exception, Barnard, 1950a, 1950b). The purpose of the present paper is to point out some of the more common variations encountered among English Bathonian lagenid species and to discuss the taxonomic and phylogenetic implications. A preliminary report has already been presented (Cifelli, 1957).

It is believed that these highly variable forms can be understood only if they are studied independently of the preconceived notions concerning the taxonomic significance of particular morphologic features. "Key" characters should be viewed with caution and evaluated in light of the total morphology of the test. Factors of distribution and continuous variation shown by transitional forms occurring in assemblages need careful consideration in delimiting species.

This does not mean that the mere recognition of intra-specific variation will solve the problem of classifying the Jurassic Lagenidae. The group is a difficult one, and a meaningful classification will require much additional study, whether variation is recognized or not. It is suggested, however, that the recognition of variable species is a more valid approach to understanding the phylogeny of the Lagenidae than the time-honored custom of giving a different name to any peculiar combination of structures that may occur in an assemblage. Evolution proceeds through variants of ancestral populations; to mask these variants with new names is to obscure important clues to the phylogeny of the group.

COMMENTS ON CLASSIFICATION OF THE LAGENIDAE

The Lagenidae dominate the Bathonian foraminiferal faunas in terms of diversity and relative abundance. Of the 104 species and subspecies recognized in this stage (Cifelli, 1959), 77 are referable to the Lagen-

idae. Species belonging to other families are generally few, and constitute insignificant parts of the assemblages. Important exceptions are the calcareous tubular specimens belonging to either *Cornuspira liasina* or *Spirillina infima*. Specimens of these species are locally abundant, and at some horizons they outnumber the Lagenidae, although they exhibit little variation.

The dominance of the Lagenidae in the Bathonian is typical of the Jurassic foraminiferal faunas, for it was during this period that the family reached its evolutionary peak. Most of the structural types of the family are already present in the Lower Jurassic (Glaessner, 1945, p. 133). Throughout the Jurassic, however, the large, diverse populations of the Lagenidae are characterized by much variation, and species and genera are not sharply defined. Practically all of the generally recognized criteria for distinguishing genera and species show a wide range of modification within a single species of Lagenidae, and the classification of individual specimens is difficult.

Most of the early work on Jurassic Foraminifera was done by Terquem who, in a sense, may be considered a lumper, since, in his series of monographs on the Système Oolithique (Terquem 1868–1870) he included numerous dissimilar forms within many of his species. However, Terquem never did really subscribe to evolutionary theory and he was strongly influenced by the catastrophic doctrines of d'Orbigny. Although he often assigned broad limits to species, he had no underlying principles to guide his classification. Most taxonomists today would consider many of Terquem's species to be a miscellany of heterogeneous specimens rather than populations of related organisms; but his illustrations do reveal a bewildering variety of lagenid forms and bring into relief the problems of classifying this difficult group.

Most later workers have given much narrower limits to species than Terquem and have erected many new species intermediate or overlapping in structure with previously described ones. A large number of lagenid species have been described from the Jurassic, but, as noted by Macfadyen (1941, p. 29), many of them have been established on inadequate grounds and are without either genetic significance or pracical value. More recently, Barnard (1950a, 1950b) and Adams (1957) have described variational patterns of some Lagenidae from the English Lias. Contrary to earlier workers, they have included a large variety of forms within the framework of a relatively few species. The recognition of variation, which involves a broader outlook of the morphological limits of species, has resulted in taxa of greater genetic significance and involves an approach which is in keeping with modern evolutionary concepts.

There is no "philosopher's stone" in taxonomy, no infallible means by which we can arrange specimens into a perfectly natural order. However, there are certain guides which can be used in classifying them into a system that most conveniently expresses their degrees of relationship in light of available information and is at the same time compatible with our present understanding of organic evolution.

The most important guide in classification is, of course, morphology. However, taxonomy is not merely a classification of morphological parts, and other factors must be considered. These other factors include the distributional patterns and the transitional aspects of the specimens. Thus, if several distinct types occur, but are connected in a single assemblage by morphologically transitional forms, it seems reasonable to assume that only one species is present.

The fact that the assemblage may include types characteristic of more than one presently accepted genus should not weaken this conclusion as the presence of transitional forms in an assemblage is strong evidence of a single population. Conversely, if two dissimilar groups of specimens with separate distributional patterns contain relatively few identical variants, they may be considered distinct species. This latter situation arises among many of the unornamented forms. The structure of the test among these species is so simple that overlapping forms are virtually indistinguishable morphologically. The associations of these with forms transitional to other types in natural assemblages provide the clues to their relationships.

In classifying the Jurassic Lagenidae, it is important to consider the total morphology of the test. There are no morphological traits which taken singly can be used as ultimate guides to classification. Glaessner (1945, p. 132) mentioned that it is unfortunate that most of the genera are based on Recent species, thus giving a narrow framework within which to place the highly variable Jurassic forms. Practically all of the morphological criteria generally recognized as important in delimiting Recent genera and species exhibit a wide range of modification within a single Jurassic species. Consequently, "key characters" such as growth plan, outline of test, shape of cross-section, sutures, and proloculus must be viewed cautiously and evaluated in light of other features of the test. When treated this way, Jurassic species are apt to be more broadly conceived than is generally the case with Foraminifera and are less amenable to treatment by morphological keys.

Among students of other invertebrate groups the tendency is to de-emphasize the significance of any single character and to consider the total morphology of the specimens and factors of distribution. Williams (1956) in a review of brachiopod morphology and classification has shown how ontogeny, shell structure, and deltidium have each at one time or other been used as a key guide to the classification of the higher categories of brachiopods, but all have proved unsatisfactory. The present trend in brachiopod systematics is to group the superfamilies according to their total resemblance.

In regard to the status of trilobite classification, Whittington (1953, p. 194) has stated, "If we can avoid being mesmerized by the importance that has so far been attached to cephalic sutures in classification, a different approach is possible, i.e., to consider all the exoskeletal characters . . . ontogeny and the distribution of genera in space and time."

Among the ammonites, the ultimate importance of suture line or position of siphuncle has been de-emphasized, and more emphasis has been placed on stratigraphic distribution of the genera. This scheme demonstrates the iterative evolutionary pattern of the ammonites; a pattern which also characterizes some of the lagenid lineages.

The problems of classification of Jurassic Lagenidae are not unique. However, there still appears to be a strong tendency to think of foraminiferal genera and species in terms of particular structures rather than populations of related organisms. Recent work on the Jurassic foraminiferal faunas (Barnard, various papers; Adams, 1957) strongly suggests that the more flexible taxonomy will better express the relationships of the Jurassic forms, at least. "Key" characters should be treated cautiously, and classification of specimens should take into consideration the totality of traits, transitional aspects of the specimens and their distributional patterns.

Although the purpose of taxonomy is to express the degrees of relationships among organisms, matters of convenience must also be considered, Consider, for example, the case of *Gryphaea*. Trueman (1922) has shown that forms of this genus have arisen independently from various stocks of *Ostrea* in the Jurassic and the Cretaceous. The evolutionary pattern is iterative, and strictly speaking each gryphaeoid form should be considered a separate genus. Few taxonomists would endorse such a scheme, however, as it would involve a large number of structurally identical genera for a relatively small group. Linnean classification has its limitations and it is doubtful that it could be used to express all of the intricate degrees of relationships in any particular group, if the phylogeny of the group were completely known. As stated by Simpson (1945, p. 17), a certain amount of compromise is necessary in classification.

In dealing with the Lagenidae we have the dubious good fortune of having to compromise very little, since the phylogeny of this family is still poorly understood. Structurally, the Jurassic forms are very similar to the Recent ones and most of the Jurassic species are referred to Recent genera. It is possible that many of these genera represent morphologic grades rather than continuous lineages. In fact, Brotzen (1953) believes that there is but distant relationship among the lagenid types of different ages and has suggested that new generic names be given "for different evolutionary stages."

Unless there are new morphologic criteria or a firm phylogenetic basis for distinguishing these genera, however, the mere addition of new names is not going to contribute to our understanding of this group. Until we have a better understanding of the existing large number of genera, artificial though they may be, it seems better to proceed within the framework of present classifications, and to avoid as much as possible the premature addition of new names.

VARIATION OF BATHONIAN LAGENIDAE

Descriptions of individual lagenid species are given elsewhere (Cifelli, 1959). Some of the more general trends in variations are summarized here. The patterns of variation can be determined only if sufficient specimens are available for a particular species. Where a species is represented by rare, isolated individuals, transitional forms are lacking and relationships cannot be reliably inferred. It might be expected that the maximum variation of a species would be observed in those assemblages in which it is most abundant. This is generally, but not entirely, the case. As was observed by Barnard (1950a, p. 383) in the Lias, variation often tends to be sporadic, without any discernible phyletic trends. Occasionally a species may occur in abundance at a particular horizon and exhibit little variation. Yet the same species at another horizon may be highly variable, though no more abundant.

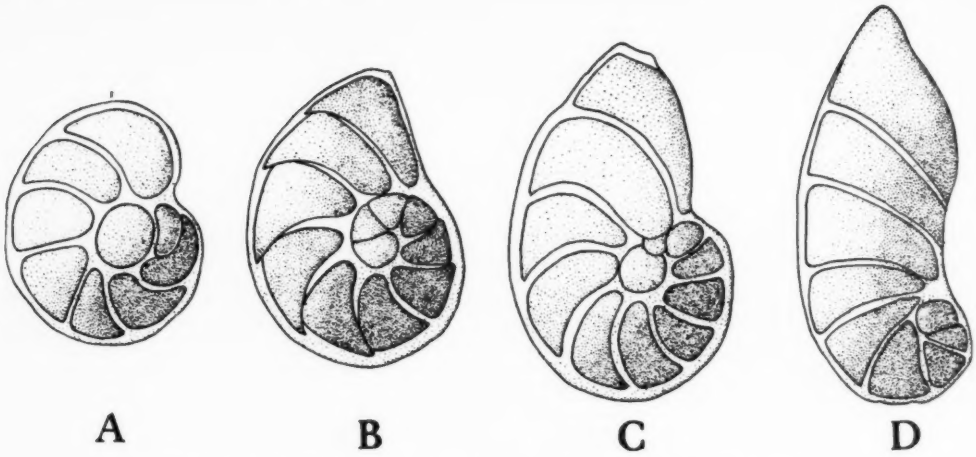
Commonly these fluctuations in the amount of variation involve separate morphologic features. For example, in the lower part of the *Wattonensis* Beds on the Dorset Coast, *Planularia beierana* (Cifelli, 1959, p. 300) exhibits a wide range of modification of the suture line, and all forms of suture from moderately depressed to limbate occur. Often, there is much variation on a single specimen. In the upper part of the *Wattonensis* Beds, exposed on the Dorset Coast, the suture line of this species is reasonably stable and on most specimens they are either flush or very slightly raised. However, the forms of the last chambers of these specimens are highly variable, and many are chevron shaped, like those of *Neoflabellina* (see below). In the overlying Upper Fuller's Earth Clay the suture line is slightly depressed and chevron chambers do not occur. The species exhibits little variation in these younger beds even though it occurs in abundance.

The morphologic variations might, of course, be attributed to migrations of similar but separate species rather than to fluctuations in the variation of a single species. Careful examination of the specimens, however, reveals that there is no adequate way of separating them into groups with mutually exclusive characters. It is highly unlikely that the same "species" splits from these assemblages would be suggested by two independent workers or that one worker's splits could be recognized by anyone else. The sporadically shifting variational pattern appears to be real, and probably reflects the genetic responses of a species to changing environmental conditions.

UNCOILING IN *LENTICULINA*

Perhaps the most common variational feature observable among the Bathonian Lagenidae is the degree of coiling in *Lenticulina* (text-fig. 1,2). In the Bathonian most representatives of this genus are tightly coiled. However, among all of the species which occur in abundance, various degrees of uncoiling are observable. In *L. munsteri*, *L. subalata*, *L. varians* and *L. tricarinella* (Cifelli, 1959) occasional variants exhibit uncoiling, with the spire composing less than one half of the test and the remainder of the chambers arranged in a linear or a gently curved series. Some of these specimens are structurally identical with *Marginulinopsis* (text-fig. 1D). On occasional specimens of *L. tricarinella* the spire is incompletely developed and the growth plan does not correspond particularly well with any previously described genera (text-fig. 2A–D; particularly text-fig. 2A).

In *L. quenstedti*, the coiling is more constant. Extreme uncoiled forms such as occur in the above-mentioned species were not observed in *L. quenstedti*, and the test of this species is always dominantly coiled. In some individuals the last one or two chambers tend to uncoil, but these chambers continue to overlap on the adoral margin. Occasionally, a more or less opposite tendency occurs in this species, in that the

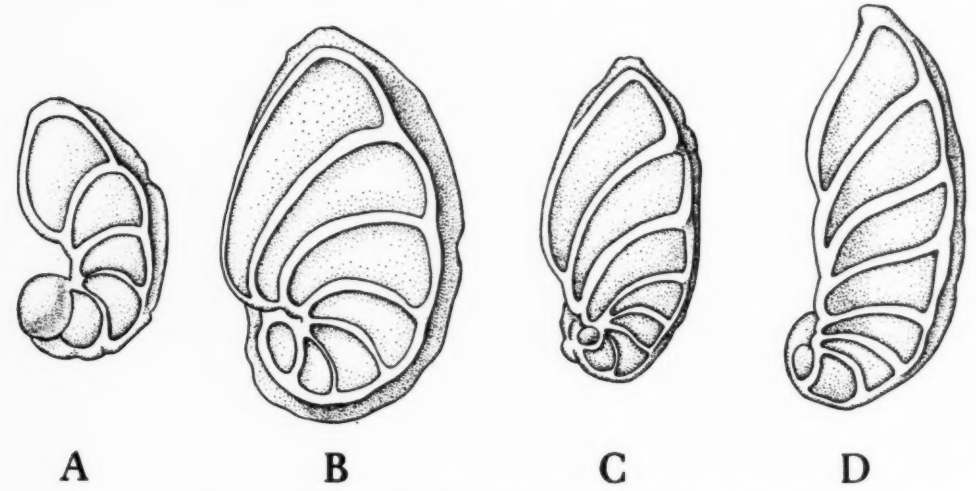


TEXT-FIG. 1—Variation in coiling of *Lenticulina munsteri* (Roemer).

later chambers sometimes tend to overlap the previous ones on the lateral margins. The resulting test is highly involute, and a new variety has been recognized on this basis (Cifelli, 1959, p. 294).

The relationships of the Jurassic species defined on an uncoiled growth plan are obscure and will remain so until topotypic suites of these species are examined. It is possible that many of them are actually variants of coiled species.

The unornamented forms are particularly difficult to place because of the simplicity of their structures. Macfadyen (1936, 1941, p. 30) and Barnard (1950b, p. 7) have included most of the Jurassic smooth uncoiled forms in *Lenticulina matutina* (d'Orbigny). However, Barnard noted that the spire of this species is identical with the adult of *L. munsteri* (Roemer). In the English Bathonian (Cifelli, 1959, p. 292), forms identical with *L. matutina* were observed to occur only as variants of *L. munsteri*. This, along with the fact that published records indicate closely parallel time and geographic distributions of *L. matutina* with *L. munsteri*



TEXT-FIG. 2—Variation in coiling of *Lenticulina tricarinella* (Reuss).

suggests that the two species are one and the same.

As a matter of fact, all uncoiled forms of *Lenticulina* observed in the English Bathonian occurs as variants of normally tightly coiled species of this genus. I have recognized no species in the English Bathonian that can be distinguished by its degree of coiling.

Some authors (e.g., Tappan, 1955; Norvang, 1957) have assigned Jurassic species to *Marginulinopsis*, a genus characterized essentially by the presence of an early coil and an elongate series of later chambers. The wide range of variation in coiling shown in Bathonian species of *Lenticulina*, however, suggests that this feature is of little taxonomic significance.

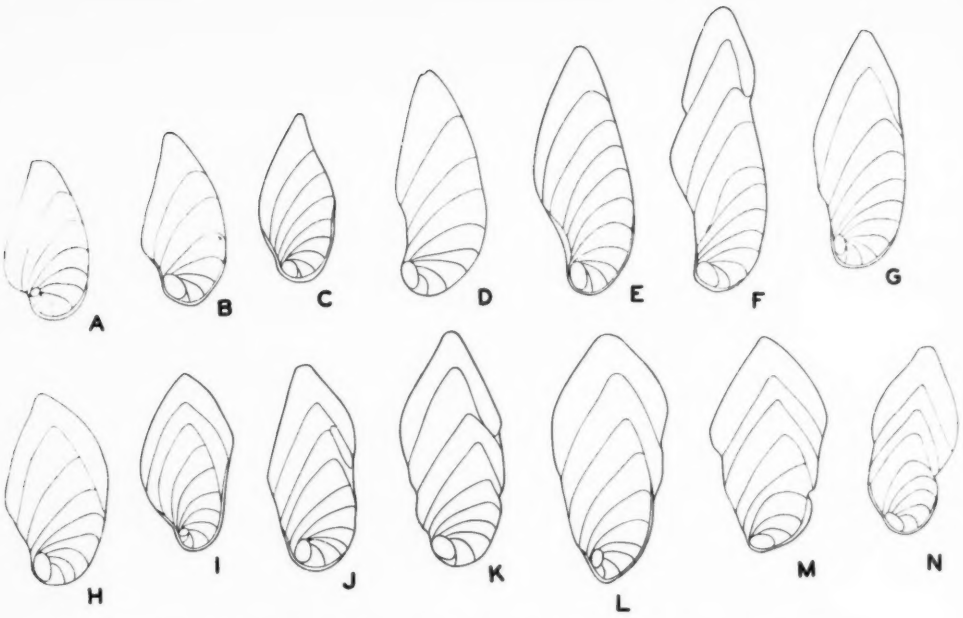
CHEVRON CHAMBERS IN *PLANULARIA*

The close similarity in the Jurassic between many coiled lagenid species and chevron chambered species variously referred to as *Flabellina*, *Neoflabellina* and *Falsopalmula* has been long recognized. Terquem observed that many species of "*Flabellina*" in the Système Oolithique were indistinguishable from species of "*Cristellaria*," except for the last chambers, which in the former genus are chevron shaped. So impressed was he with the resemblance that he even applied the same specific name to species of the two different genera, e.g. *Cristellaria anomala*, *Flabellina anomala; Cristellaria semiinvoluta*, *Fabellina semiinvoluta*. He believed that this simplified identification although he did not intend to imply any relationships by this scheme.

The possibility that these forms might be closely related seems to have been largely ignored until Bartenstein (1948, p. 124) established the genus *Falsopalmula* for the Jurassic chevron chambered forms and showed that each species of this genus is closely related to, and derived from, a species of *Planularia*. By definition, the genus is polyphyletic. In a study of the Lias of Byfield Barnard (1950b) included chevron chambered forms in both *Planularia pauperata* Jones and Parker and *Lenticulina varians* (Borneman). Adams (1957, p. 219) observed a close parallel in the variational patterns of *Planularia* and *Falsopalmula* in the Upper Lias of Lincolnshire. Although Adams followed the conventional taxonomic procedure and assigned all of the chevron chambered forms to the genus *Falsopalmula*, he concluded: "The variation seen in *Falsopalmula* parallels that of *Planularia* so closely as to suggest that, bearing in mind Bartenstein's earlier evidence, almost any species of *Planularia*, at least in the Upper Lias, may produce equitant chambers and thus become a *Falsopalmula*."

In the English Bathonian chevron chambers occur in variants of *Planularia beierana*. In some specimens these chambers are well established, and on the basis of this single morphological feature would be referable to the genus *Falsopalmula*. However, the chambers are very irregular in their development, and on many specimens they are only partially formed. This is shown in specimens from the *Wattonensis* Beds from the Dorset Coast which are illustrated in text-figure 3, and all are from a single sample. The number of chevron chambers on the specimens varies between one and three. On some specimens they are symmetrical with both arms of the chevron being of equal length, while in others they are asymmetrical, because of the unequal overlap on the two margins of the test. Often the symmetry of the chevrons varies on a single specimen. The chevrons form either by progressive overlap of one arm on the oral margin, or by a sudden change in the growth plan, with an abrupt overlap on the oral margin. The suite of specimens shows the irregularity in form of these chevron chambers, and reflects the instability of the character within the population. In other samples, occasional specimens are found in which the chevrons are highly symmetrical, and occupy the greater portion of the test. These forms are identical with many of the figured specimens of *Falsopalmula deslongchampsi* (Terquem). However, such specimens were always found to be associated with *Planularia beierana*, and it appears that, in most cases at least, genetic continuity existed between the two forms.

The published records of the chevron chambered forms in the Jurassic indicate that they are intimately associated with species of *Planularia* or *Lenticulina*. The conclusion, therefore, is that the genus



TEXT-FIG. 3—Variation of *Planularia beierana* (Gumbel) showing the occurence of chevron shaped chambers in some variants.

Falsopalmula is a morphological type and includes variants of several distinct species. As far as can be determined, forms with this chamber arrangement did not split off from their parent populations during the Jurassic except, perhaps, in rare instances. This qualification is made because occasional chevron chambered forms are found in the Bathonian which cannot be shown to be transitional to *Planularia*.

In the rare instances where this has been thus far observed the total number of specimens was small so that the absence of transitional forms may have been due to collection failure. But there is also the intriguing possibility that these may record cases where chevron forms did actually lose genetic continuity with the parent populations and split into separate species. More data are needed from closely spaced samples in continuous sections. With the aid of biometrics a detailed study of these forms may yield information of fundamental importance concerning the evolutionary patterns of Foraminifera.

The fact that specimens corresponding in structure to the genus *Falsopalmula* occur in species of *Planularia* results in an awkward problem of taxonomy. The manner in which the problem is treated depends largely on one's own particular philosophy. From a phylogenetic point of view a good guide in such circumstances is a point of taxonomy emphasized by Simpson (1945, p. 17), "The animals assigned to a given group are more closely related to each other than they are to the members of other groups of equal rank." In view of this and all that has been said previously there seems to be no need for the genus *Falsopalmula;* for the present, at least, the relationships of the chevron forms can be better expressed by including them in species of *Planularia*. If it should be later discovered that phyletic groupings of chevron chambered forms do exist in the Jurassic, then, of course, the matter would have to be reconsidered.

What would appear to be a different philosophy was expressed by Tappan (1955, p. 54) who took exception to Barnard including chevron forms in *Lenticulina varians* and stated, "it is legally impossible to con-

sider a single species as belonging to two genera or subgenera." If genera and species are considered from a purely morphologic point of view, there is merit to this objection. However, the splitting of a natural transitional assemblage into two artificial genera does not seem to me to be in the best interests of taxonomy.

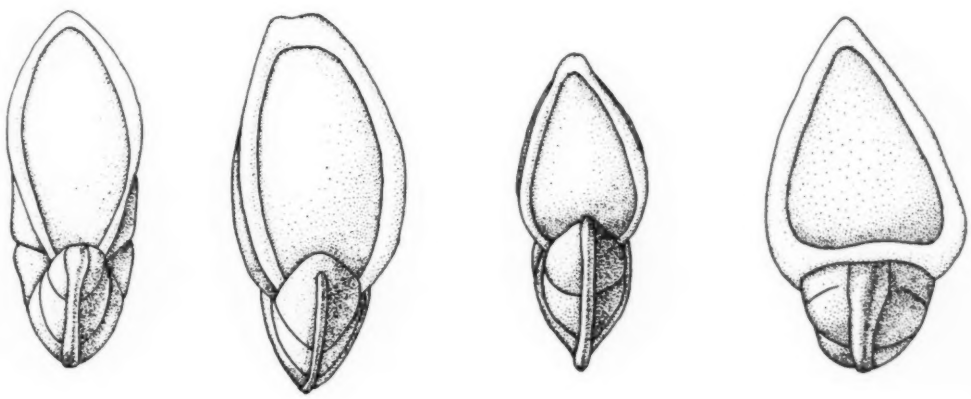
TROCHOID CHAMBERS IN *LENTICULINA*

In certain variants of *Lenticulina sowerbyi* (Schwager) and *L. turgida* (Schwager), occurring in the English Bathonian, the last chamber overlaps on to one side of the preceding chamber, resulting in a trochoid growth plan characteristic of *Darbyella*. Tappan (1955, p. 51) assigned trochoid forms from the Upper Jurassic of the Arctic slope to this genus (*Darbyella volgensis* Tappan), but noted that many species in the Jurassic and Lower Cretaceous are gradational between *Lenticulina* and *Darbyella* so that the two genera may be synonymous. The Jurassic forms, however, have radiate apertures while *Darbyella* was defined as having an aperture with an elongate slit. To my knowledge the slit-like aperature does not occur in any of the Jurassic coiled lagenids. This difference in the nature of the aperture provides a possible means of distinguishing the homeomorphous Jurassic forms from *Darbyella*, a genus that does not appear until the Cretaceous and was probably derived from *Robulus*.

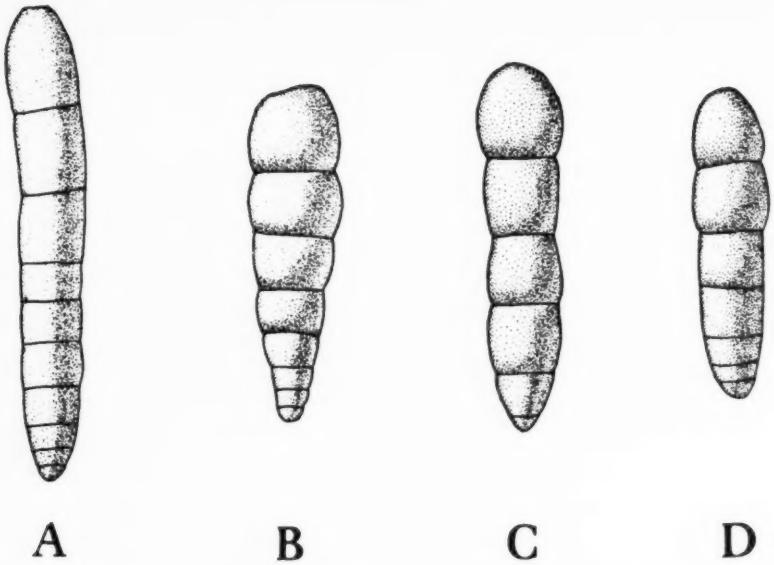
TRIANGULAR CROSS-SECTION IN *LENTICULINA*

Adams (1957, p. 206) has discussed the variable nature of cross-sectional shape in the lagenids occurring in the English Lias. In the Bathonian, marked modifications in cross-section occur in *Lenticulina galeata* (Terquem) and *Lenticulina tricarinella* (Reuss). Both of these species are normally rather compressed in cross-section, the margins of the test being more or less parallel. This is particularly true of *L. tricarinella; L. galeata* is generally slightly biconvex in cross-section. Occasionally, marked variation in this morphological feature occurs, and both species include variants which are triangular in cross-section, as is characteristic of the genus *Saracenaria* (text-fig. 4).

Isolated specimens of these variants might be called *Saracenaria* sp., except for the fact that they have been observed in large populations and the relationships can be reliably inferred. This modification is not common in the Bathonian and *Saracenaria*-like specimens are rare, even among large suites of specimens. It is, however, an example of a structural type occurring in two distinct species, neither of which species was seemingly ancestral to those characterized by triangular cross-sections.



TEXT-FIG. 4—Variation in shape of cross-section of *Lenticulina galeata* (Terquem).



TEXT-FIG. 5—Variation in shape of chambers of *Pseudonodosaria hybrida* (Terquem and Berthelin).

To complicate matters there occurs in the Bathonian *Saracenaria triquetra* (Gumbel), which is a distinctive form, and seemingly unrelated to any species of *Lenticulina* observed in the Bathonian. *Saracenaria triquetra* is consistently triangular in cross-section and is known from strata as old as Lias. Whether individual triangular specimens belong with species of *Lenticulina* or *Saracenaria* can only be determined by studies of suites of specimens. The situation is admittedly awkward, and identification of isolated specimens depends on the judgment and experience of the investigator.

Uncoiled forms of *Saracenaria* are sometimes placed in the genus *Saracenella*. As previously shown, however, the degree of coiling is an extremely variable character and unreliable taxonomically. At any rate, Cushman (1948, p. 218) has pointed out that the type of *Saracenaria* is apparently an uncoiled form, and the two genera are, therefore, synonyms.

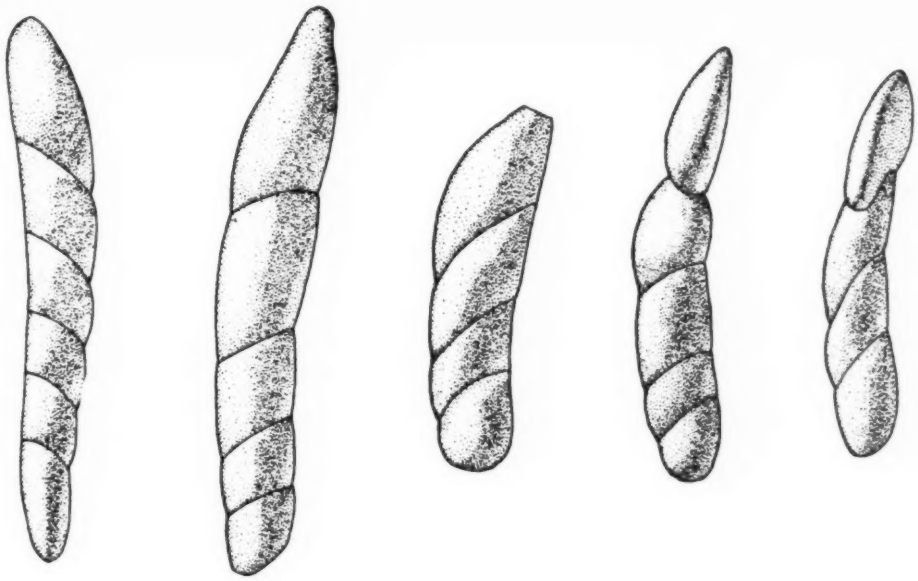
NODOSARIA-PSEUDONODOSARIA COMPLEX

Barnard (1950b, p. 26) described the variation in shape of chambers during growth of individuals of *Pseudonodosaria vulgata* (Borneman). The shape of the chambers varies from pupiform, which is typical of the genus, to nodosarine; in some specimens the chambers are dominantly nodosarine and the specimens are indistinguishable from species of *Nodosaria*. According to Barnard (1950, p. 26), forms similar to *P. vulgata* and with similar variational patterns occur in the Gault of the Cretaceous. Barnard does not believe that there is close relationship between these forms and those of the Lias, but, instead, he regards the similarity as a form of mimicry.

In the Bathonian the same kind of variation occurs in *Pseudonodosaria hybrida* (Terquem and Berthelin), shown in text-figure 5. Pupiform chambers are the most common among individuals, otherwise the species might just as well be referred to *Nodosaria*.

A somewhat similar pattern of variation occurs in *Nodosaria opalini* Bartenstein. This species is common in the Bathonian of England and is easily recognized by its fine longitudinal costae. Both nodosarine and pupiform chambers occur (Cifelli, 1959, p. 315), but the nodosarine ones are dominant and the species is referred to the genus *Nodosaria*.

Pupiform chambers were also observed



TEXT-FIG. 6—Variation in chambers of *Dentalina intorta* Terquem, showing axial twist of last chamber in variants.

in *Dentalina propinqua* (Cifelli, 1959, p. 311). This species is also common in the English Bathonian, but its generic position is problematic. It is placed in *Dentalina* because the test is most often arched, and the chambers are generally constricted. The sutures, however, are usually transverse, as in *Nodosaria*, and, as mentioned, pupiform chambers do occur occasionally. To further complicate matters, the test often exhibits much compression, and the aperture is only faintly radiate. Both of these features are characteristic of Jurassic *Lingulina*. The species, then, contains specimens which, on the basis of morphology, might possibly be assigned to any of four different genera. It is placed in *Dentalina* because of the dominance of dentaline features.

The relationship of these species is obscure and the choice of a genus for each of the species is based on the most common occurring type. This is an unhappy compromise to our present state of knowledge. What is needed is a thorough analysis of these forms at the species level from Lower Jurassic and older rocks. Ultimately, it may be possible to realign the genera to fit phyletic groups of species.

AXIAL TWIST OF LAST CHAMBER IN *DENTALINA*

The genus *Dentalina* is characterized by an arcuate test with the chambers arranged in a linear series. The test is compressed to some degree and the chambers are arranged along a common longitudinal axis. In *Dentalina intorta* Terquem, the last chamber is highly variable, and in some specimens the axial plane of this chamber lies at an angle to that of the preceding one (text-fig. 6). The angle is variable, but generally it is less than 90°. Although *D. intorta* is common throughout much of the English Bathonian, this twist of the last chamber occurs but occasionally (in perhaps 2% of the specimens). It was observed in specimens from the Forest Marble of the Dorset Coast, the Upper Fuller's Earth of Somerset and the Fuller's Earth of Oxfordshire. The twisting in *Dentalina intorta*

was also observed in a specimen of this species in the Terquem collection at the Musée d'Histoire Naturelle, which had been collected by Terquem from the Fuller's Earth at Metz. This variational feature, then, characterizes the species over a broad geographical extent, though it occurs but rarely in individual populations.

The twisting of the axial plane in *Dentalina intorta* is reminiscent of the growth plan of the early Polymorphinidae, in which the chambers of the test are arranged in a spiral series, with each succeeding chamber added at an angle to the preceding one. In *D. intorta*, only the last chamber deviates in angle from the preceding, and no spiral is actually produced. Fundamentally, the difference is that in the Polymorphinidae the spiral growth plan occurs early in the ontogeny while in *D. intorta* it begins in the very last stages of growth and probably lacks the opportunity to fully develop.

According to Cushman (1948, p. 221) and Glaessner (1945, p. 133) the Polymorphinidae were probably derived from a coiled lagenid ancestor early in the Jurassic, or possibly in the Triassic. It is not suggested here that the Polymorphinidae were derived from *Dentalina*, but the twist in axial plane of the last chamber in *D. intorta* suggests that the spiral growth plan may have occurred in more than one lineage of Lagenidae. It is indicative of the genetic plasticity of this family and of the kinds of parallelisms that are possible.

LINGULINA AND *FRONDICULARIA*

Two closely related genera are *Lingulina* and *Frondicularia*. These genera are distinguishable from each other only by the shape of the suture, which is transverse in *Lingulina* and chevron-shaped in *Frondicularia*. For the most part, the sutures are distinctly of one or the other type and specimens are readily assigned. There is overlap, however, and that species of the two genera are closely related is indicated by the similar variational patterns (Cifelli, 1959, p. 326).

Barnard (1956, p. 271) observed that all specimens of *Lingulina* from the English Lias began with a spherical proloculus and failed to reveal a coiled microspheric proloculus. This is also true of the Bathonian *Lingulina* and *Frondicularia*. In addition, the apertures of both forms are variable, and include rounded as well as radiate forms. They differ, therefore, from their more modern counterparts in this respect and may possibly be homeomorphous forms. As with other lagenids, the determination of relationships will require a thorough stratigraphic analysis at the species level, in this case involving forms intermediate in age between the Jurassic and the Recent.

SIGNIFICANCE OF VARIATION

The fact that most of the structural types of the Lagenidae are present in the Lower Lias is an indication that much of the evolution of this family occurred before the Jurassic. Foraminiferal faunas from the Triassic are notably meager, but there are many similarities between them and those of the Jurassic. Consequently, many of the ancestral forms of the Lagenidae are to be sought in Triassic and probably older rocks.

The great diversity and abundance of the Lagenidae relative to the other Foraminifera in the Jurassic indicates that they were still undergoing divergence and adaptive radiation at this time. Characteristic of organisms in the early period of their evolutionary development, they exhibit a low degree of morphological stability. This is reflected in the morphology of the test, which is highly variable within the limits of a single species.

Many variants of particular species contain morphologic features diagnostic of later, or sometimes, contemporary genera. This, actually, is what one would expect to occur among ancestral forms, as variation provides the "building blocks" of evolution, and the structural types characteristic of of genera should occur first as variations among ancestral species. It might also be expected that within an evolving group of organisms similar mutations would occasionally arise among related but distinct lineages, producing similar morphologic variants. Furthermore, if the mutations are recurrent, it is probable that the same variants would appear time and time again in the same lineage or closely related lineages. The fate of such variants would depend largely on factors of natural selection. It is important that taxonomy should, to a de-

gree, reflect this variation, or else it will not be compatible with the evolutionary history of the group.

It would be of interest to known something about the source of the variation revealed by the Lagenidae. This, however, involves factors of genetics, and knowledge of living Foraminifera is still quite limited. The importance of studying living species as an aid in evaluating the taxonomic significance of variations has already been stressed by Arnold (1953). The observations that Arnold (1954) has made on the chitinous Foraminifera *Allogromia laticollaris* are revealing. A living culture of this species yielded descendents with most of the basic growth patterns of Foraminifera as well as wide variation in apertural characters and body shapes. Arnold has suggested that the procedures used in the study of *Allogromia laticollaris* might be used to determine variation of more complex species. It may well be that many Foraminifera are much more plastic in their genetic constitution than is generally allowed for, and living Foraminifera may be potentially capable of wide ranges of variation.

The structural types of lagenid genera probably became established from variations among ancestral species as a result of adaptations to new modes of life. However, the functional significance of the morphological features of foraminiferal tests are virtually unknown. Quite possibly many of the test features are genetically linked characters and are external expressions of physiological factors.

An interesting characteristic of the Jurassic Lagenidae is the scarcity of discernible phyletic trends. A few have been described from the Lias by Bartenstein and Brand (1937), Barnard (1956) and Norvang (1957), but for the most part these are based on local successions and it is doubtful if many of these represent true evolutionary sequences. The best documented one appears to be the *Lingulina tenera* "plexus." Similar evolutionary trends of this form in the Lias were observed by Barnard (1956) in England and Norvang (1957) in Jutland. The species does not occur in the English Bathonian. Many other phyletic trends described cannot be confirmed elsewhere, and they may possibly reflect local population shifts, not representing persistent trends.

Most often the variational aspects of a particular species change considerably from one assemblage to the next, without any apparent trends. To some degree these changes probably reflect genetic responses of a population to changes in environment. Arkell and Donovan (1952) have discussed the cyclic nature of the Great Oolite deposits, and so there is good evidence for constantly changing environmental conditions in the Bathonian, at least.

Despite the fluctuations in environment during the Jurassic, selection pressure for the Lagenidae was probably at a minimum during that time. Other foraminiferal families had few representatives, belonging mostly to primitive genera, in the Jurassic, and must have offered little competition. Low selection pressure, due to little competition, might possibly be responsible for the high degree of variation exhibited by the Lagenidae. Undoubtedly lagenids inhabited a great range of environmental niches in the Jurassic, as they do today, and because of the lack of competition they dominated most of the environments. After the Jurassic, other families evolved rapidly and must have seriously competed with the Lagenidae. As a result, the post-Jurassic lagenids seldom dominate the assemblages in which they occur, and generally exhibit less variation, even though they are still widely distributed.

ANCESTRY OF THE LAGENIDAE

There has been much divergence of opinion concerning the ancestry of the Lagenidae. Probably most students of Foraminifera have considered *Lenticulina*, or similar coiled forms, to be the most primitive (Glaessner, 1945, p. 133). Chapman, Howchin and Parr (1934) have held an opposite view, and considered that the Lagenidae evolved from a straight or openly curved form. Their conclusion was based on a study of Permian Foraminifera from Australia, where closely coiled forms appeared to be absent. The problem of lagenid origin and evolution has been recently reviewed by Norvang (1957, p. 32) who believes that the coiled forms are derived from the uncoiled ones. Norvang's convictions are based largely on his study

of Lias forms of Jutland. Norvang observed that no forms of *Lenticulina* occur in the basal Lias, and that the Lias species of *Lenticulina* appear to have developed gradually from *Marginulina* (Norvang, 1957, p. 30).

From the observations of Barnard (1950a) however, it would appear that comparable trends do not exist in the Lias of the Dorset Coast, England. Although *Lenticulina* was not recorded from the lowermost zone there, it was recorded in abundance in the *Angulatum* Zone, which is low in the Lias. Furthermore, Barnard emphasized the central tendency of the coiled form, from which the uncoiled types appear as variants. Certainly, there is no indication of a progression from uncoiled to coiled type. Quite probably the trends noted by Norvang from the Lias of Jutland are local, and are not of general phylogenetic significance.

One of the chief reasons for considering the linear forms as primitive has been the absence of coiled types in systems older than Jurassic. Recently, however, species of *Astacolus* and *Lenticulina* have been described from the Triassic of Alaska (Tappan, 1951) and the Permian of Australia (Crespin, 1958).

The existing data on the pre-Jurassic Lagenidae are too meager to justify any significant conclusions concerning the early ancestry of the family. Whether the earliest forms were coiled or straight, it seems doubtful that the structural types of the later genera originated by a progression of transitional forms from one to the other. The variational patterns exhibited by the Jurassic species show that identical structural types may originate independently from distinct lineages and at different times. Evidence for phyletic trends from one morphological type to another is unconvincing. On the other hand, individual populations exhibit a wide range of modification in test morphology, and it is not uncommon to find structural types (such as growth plan) characteristic of more than one genus within a single species.

The structure of the lagenid test is relatively simple, and the number of morphological modifications are limited. There is much variation, but the variation is based on relatively few themes. There can be no doubt that when viewed in detail many of the genera as generally conceived are polyphyletic. To clarify the phylogeny of the Lagenidae detailed studies of the whole family are needed which include representatives of all ages. Moreover, the role of variation in the evolution of the group should not be overlooked, and variants should not be disguised with separate generic names.

BIBLIOGRAPHY

ADAMS, C. G., 1957, A study of the morphology and variation of some Upper Lias Foraminifera: Micropaleontology, v. 3, p. 205–226, text figs. 1–26.

ARKELL, W. J., and DONOVAN, D. T., 1952, The Fuller's Earth of the Cotswolds and its relation to the Great Oolite: Geol. Soc. London, Quart. Jour., v. 107, p. 227–253.

ARNOLD, Z. M., 1953, Paleontology and the study of variation in living Foraminifera: Cushman Found. Foram. Res., Contrib., v. 4, p. 24–26.

——, 1954, Variation and isomorphism in *Allogromia laticollaris:* a clue to foraminiferal evolution: Cushman Found. Foram. Res. contrib., v. 5, p. 78–87.

BARNARD, T., 1950a, Foraminifera from the Lower Lias of the Dorset Coast: Geol. Soc. London, Quart. Jour., v. 105, p. 347–391, text figs. 1–11.

——, 1950b, Foraminifera from the Upper Lias of Byfield, Northamptonshire: Geol. Soc. London, Quart. Jour., v. 106, p. 1–36, text figs. 1–17.

——, 1956, Some Lingulinae from the Lias of England: Micropaleontology, v. 2, p. 271–282, pls. 1–3.

BARTENSTEIN, H., 1948, Taxonomische Abgrenzung der Foraminiferen-Gattungen *Palmula* Lea, *Flabellina* d'Orbigny, und *Falsopalmula* n.g., gleizeitigeine Revision der Jura-Arten von "*Flabellina*": Senckenbergiana, v. 28, p. 119–137, pls. 1,2, text figs. 1–5.

BARTENSTEIN, H. and BRAND, E., 1937, Mikropaläontologishe Untersuchungen zur stratigraphie des nordwestdeutschen Lias und Doggers: Senckenb, naturf. Gesell., Abh. 439, p. 1–224, pls. 1–20, text figs. 1–20, 5 tables.

BROTZEN, F., 1953, Problems in the nomenclature of the Foraminifera: Micropaleontologist, v. 7, p. 35–38.

CHAPMAN, F., Howchin, W. and Parr, W. J., 1934, A revision of the nomenclature of the Permian Foraminifera of New South Wales: Roy. Soc. Victoria, Proc., n.s., v. 47, p. 175–189.

CIFELLI, R., 1957, Variation aspects of some Bathonian (Middle Jurassic) Lagenidae (abstract): Geol. Soc. America Bull., v. 68, p. 1709.

——, 1959, Bathonian Foraminifera of England: Mus. Comp. Zoology Bull., v. 121, no. 7, p. 263–368, pls. 1–7.

CRESPIN, I., Permian Foraminifera of Australia:

Bur. Min. Res., Geology and Geophysics Bull. 48, p. 5–129.

CUSHMAN, J. A., 1948, Foraminifera, their classification and economic use: Harvard Press, 4th ed., 605 p., 54 pls.

GLAESSNER, M. F., 1945, Principles of Micropaleontology: Melbourne Univ. Press, 296 p. 14 pls.

MACFADYEN, W. A., 1941, Foraminifera from the Green Ammonite Beds, Lower Lias, of Dorset: Roy. Soc. London, Phil. Trans., ser. b, Biol. Sci., no. 576, v. 231, p. 1–73, pls. 1–4.

NORVANG, A., 1957, The Foraminifera of the Lias Series in Jutland, Denmark: Copenhagen, 135 p., 16 pls.

SIMPSON, G. G., 1945, The principles of classification and a classification of Mammals: Amer. Mus. Nat. History, Bull., v. 85, p. 1–350.

TAPPAN, H., 1951, Foraminifera from the Arctic slope of Alaska. General Introduction and Part I. Triassic Foraminifera: U. S. Geol. Surv. Prof. Pap. 236-A, p. 1–20, pls. 1–5.

——, 1955, Foraminifera from the Arctic slope of Alaska. Part II. Jurassic Foraminifera: U. S. Geol. Surv. Prof. Paper. 236-B, p. 21–90, pls. 7–28.

TERQUEM, O., 1868, Premiere Mémoire sur les Foraminifères du système Oolithique Etude du Fullers-Earth de la Moselle: Soc. Hist. Nat. Moselle, Bull., v. 11, p. 1–138, pls. 1–8.

——, 1870, Deuxième Mémoire sur les Foraminifères du système Oolithique zone a *Ammonites parkinsoni* de la Moselle: Acad. Imp. Metz, Mém., v. 50, p. 403–456, pls. 9–21.

——, 1870, Troisième Mémoire sur les Foraminifères du système Oolithique comprenent les genres *Frondicularia*, *Flabellina*, *Nodosaria*, *Dentalina*, etc., de la zone à *Ammonites parkinsoni* de Fontoy (Moselle): Acad. Imp. Metz, Mém., v. 51, p. 299–380, pls. 22–29.

TRUEMAN, A. E., 1922, The use of *Gryphaea* in the correlation of the Lower Lias: Geol. Mag., v. 59, p. 256–265.

WHITTINGTON, H. B., 1954, Arthropoda: Trilobita, in Kummel, Status of invertebrate paleontology: Mus. Comp. Zoology Bull., v. 112, p. 193–199.

WILLIAMS, A., 1956, The calcareous shell of the Brachiopoda and its importance to their classification: Biol. Reviews, v. 31, p. 243–287.

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PERMIAN CORALS FROM NEVADA AND CALIFORNIA

W. H. EASTON
University of Southern California, Los Angeles 7, California

ABSTRACT—Seven species of rugose corals are described from Permian (mostly Leonard Series) strata in the Basin and Range Province of Nevada and California. *Caninia trojana, Lithostrotionella mokomokensis, Lithostrotionella dilatata, Diphyphyllum connorsensis, Thysanophyllum princeps, Lonsdaleia illipahensis,* and *Lonsdaleia cordillerensis* are named. The corals occur in thick successions of commonly cyclical alternations of limestone and sandstone near the eastern margin of the Cordilleran geosyncline. Local distribution and biostromal development can be used in subdividing and mapping the Permian strata of east-central Nevada.

INTRODUCTION

THICK deposits of marine strata of Permian age crop out in the Basin and Range Province in California, Nevada, and Utah. Although paleontologists have devoted some attention to the fusulinids in these Permian beds, much more descriptive work is needed on all phases of paleontology. The purposes of this paper are to describe some species of corals from the area and to show their stratigraphic occurrence in the Permian System.

Permian corals have been discovered infrequently in North America, partly because of the restricted nature of Permian seas and partly because of seemingly adverse environments for growth of corals in those seas. Known Permian faunas include several corals which have been described from the midcontinent by Moore & Jeffords (1941), who also (1941, p. 67,68) review the previous works in that area. Permian corals from British Columbia have been described by Smith (1935); from Oregon, by Merriam (1942); and from California, by Langenheim & McCutcheon (1959).

Corals are locally very abundant in Permian strata of the Basin and Range Province. Indeed, they may comprise biostromes a foot or more in thickness. Moreover, some species are widespread, ranging north-south over a distance of at least 500 miles from northeastern Nevada to southeastern California. It is probable that the corals occupy an east-west zone at least 200 miles wide in the region between the Confusion Range of west-central Utah and the Eureka district of east-central Nevada. Thus, a coralline facies of the marine Permian strata seems to have been deposited along the eastern or continental side of the Cordilleran geosyncline.

It has been the good fortune of the writer to be able to study and to collect from numerous successions of Permian strata in the Cordilleran region. This work was begun in 1947 and has continued through most of the succeeding summers. During parts of five summers the writer was engaged in mapping with students enrolled in the summer field geology courses conducted by the University of Southern California in White Pine County, Nevada. Several summers were spent in paleontologic and stratigraphic studies of Permian and other strata on other projects. It is a pleasure to acknowledge my indebtedness to numerous students, faculty colleagues, and to various other geologists for assistance in the field work. Collections described herein which were originally made in the course of field investigations for Union Oil Company of California have been deposited at the University of Southern California through the kindness of Dr. J. C. Hazzard.

STRATIGRAPHY

Corals are described from two Permian localities in the southern part of the Basin and Range Province. The detailed stratigraphic succession of Permian rocks in the Providence Mountains of southeastern California has been published by Thompson & Hazzard (1946), and the general sequence of Permian strata in the Spring Mountains of southwestern Nevada has been discussed by Longwell & Dunbar (1936).

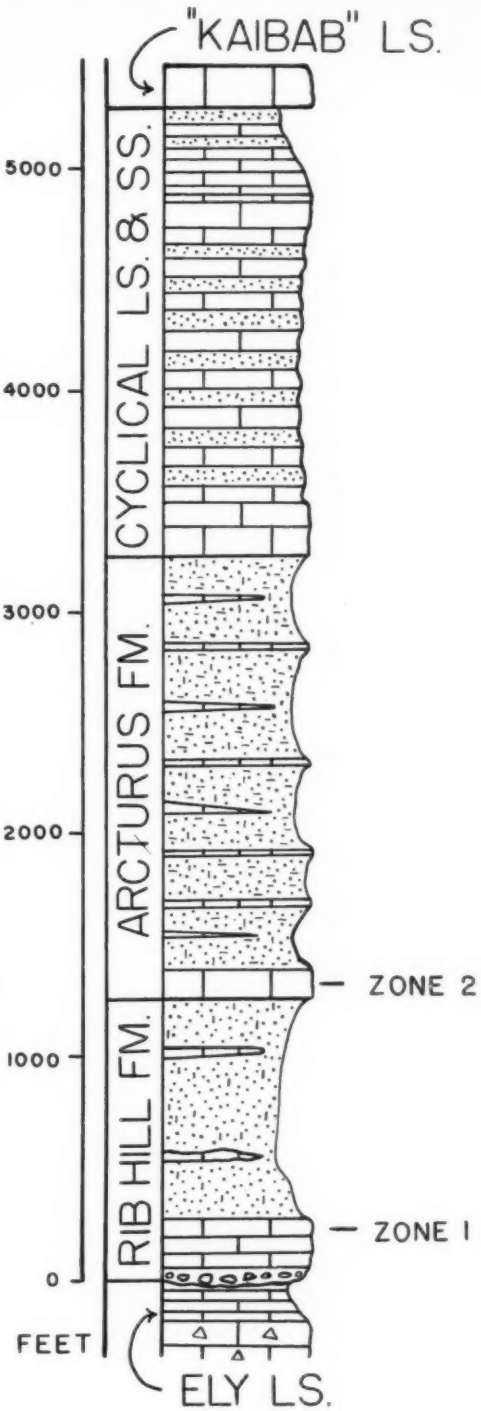
Only part of the thick Permian succession in east-central Nevada has been published

in detail. Knight (1956) has published graphic sections of two stratigraphic successions of Leonard strata in White Pine County. Additional detailed measurements are available for somewhat lower strata in the same county through unpublished research by Ehring (1957). Most of the corals to which reference is made herein were collected from Permian strata in White Pine County.

The Permian succession in east-central Nevada is one of the thickest discovered in North America. It is possible that over 7000 feet of Permian strata are represented there, of which at least 5000 feet are referable to latest Wolfcamp and Leonard Epochs. Corals have not been discovered in the latest Leonard or in the Guadalupe strata in the areas studied.

The Permian succession pertinent to this report is depicted schematically in text-figure 1. Thicknesses are only approximated because the section is a composite of outcrops at several localities. The region is one of considerable structural complexity, in addition to which the western outcrops in the region represent a more carbonate-rich facies than is present in the eastern outcrops. Solution of some perplexing structural and stratigraphic problems has been materially assisted by use of corals in a block of quadrangles consisting of the Ely, Illipah, Illipah 1 advance sheet, Treasure Hill, Pancake Summit, Green Springs, and Buck Mountain quadrangles.

The most nearly complete and readily accessible locality in which the Late Paleozoic rocks can be studied in the area lies along U. S. Highway 50 in the east half of the Illipah quadrangle, about 30 miles (airline) west of Ely, Nevada. The Illipah section has been studied by many geologists engaged in exploratory programs of oil companies in Nevada between 1948 and the present. The section lies within the region mapped during several summers by students at the summer field geology camp of the University of Southern California.



TEXT-FIG. 1—Schematic and composite stratigraphic section of the coral-bearing Permian strata in White Pine County, Nevada.

Permian strata in the area rest with apparent concordance upon the Ely limestone of Early Pennsylvanian age. The Ely limestone consists of about 1500 feet of massive to platy, grey limestone. Detailed information on the stratigraphy and paleontology of the Ely limestone will appear in a future number of this journal in an article by Bernard O. Lane.

The basal unit of Permian rocks mapped by us is the Rib Hill formation. Its lower limit is determined by the presence of a thin, chert pebble conglomerate. The succeeding limestones account for as much as 300 feet of section at some localities, but more generally only the uppermost bed of coralline limestone about 30 feet thick is present. This massive unit locally is almost a biostrome of colonial corals. It comprises zone 1 of the coral succession. The remainder, and principal part, of the Rib Hill formation consists of pink to yellow sandstone in the eastern facies but becomes increasingly calcareous and evenly buff in color westward. The arenaceous portion of the Rib Hill formation is about 1000 feet thick.

The Arcturus formation overlies the Rib Hill formation conformably and comprises about 2000 feet of strata. In its eastern facies near the type section (as on the west grade leading up to Murry Summit) the Arcturus formation consists of numerous beds of pink to yellow sandstone intercalated with grey limestone in crudely cyclical alternations. The western facies, however, is even less cyclical in appearance and the sandstones are more uniformly buff and are very calcareous. Toward the western margin of the mapped areas the Rib Hill and Arcturus formations become difficult to differentiate. The base of the Arcturus formation, however, is a widespread, massive succession of limestones which contain biostromes of corals referred to herein as zone 2. Corals occur less abundantly in other limestone beds within the Arcturus formation, particularly in the lower strata.

The uppermost strata containing corals discussed herein comprise a strikingly cyclical sequence of criquina, grey sandstone, and fusulinid-rich, buff limestone. The whole succession produces prominent cliffs and bench-and-bluff topography in the high ridge north and south of Moorman Ranch in the Illipah quadrangle. It is probable that this un-named unit is 2000 feet thick, although the upper part is inadequately known. Knight (1956) has published on the fusulinids in the succession. Corals occur in some of the limestone beds.

Overlying the foregoing sequence at some places is a massive, white limestone about 200 feet thick. It is referred to in text-figure 1 as the "Kaibab" limestone because of its position in section. It occurs between strata of Leonard age and strata containing the Phosphoria fauna. Corals are not known from so-called Kaibab limestone.

FAUNAL ANALYSIS

The most unusual feature of the Permian coral fauna from the Basin and Range Province is the abundance of compound corals belonging to groups with a tendency for the development of some sort of axial structure. In *Lithostrotionella* and *Lonsdaleia* the axial structure may be conspicuous, whereas it is reduced in *Diphyphyllum* and is absent in *Thysanophyllum*. *Lithostrotionella* is noteworthy because this genus is widespread in Meramec strata (Middle Mississippian) from the Appalachian to the Cordilleran ranges. On the other hand, *Lithostrotionella* has been reported from Pennsylvanian and Permian strata of several countries, including Canada (Smith, 1935). Merriam (1942) was the first to report *Lithostrotionella* from Permian strata in the United States (Leonard of Oregon).

A second notable feature is the localized abundance of very large specimens of *Caninia*. *Caninia* is common in Late Paleozoic strata in many regions of the world, including North America, but never before (to the writer's knowledge) did species attain the breadth of the species described hereafter.

A third, but negative, phenomenon is the apparent absence of species of *Waagenophyllum* in the collections. *Waagenophyllum* is widespread in Leonard strata of other countries, and has also been reported from Oregon and British Columbia. Perhaps its presence will be proved by slicing of specimens from future collections in the Basin and Range Province.

Faunal elements associated with the corals are meager. Fusulinids may be

locally abundant in coralline beds, but at other localities they are absent. A few specimens of the large gastropod, *Omphalotrochus*, have been collected, particularly in the Arcturus formation. *Dictyoclostus ivesi* also occurs here and there in these Leonard strata, but is rarely common. At a few localities large, ramose fronds of stony bryozoans and the spines and plates of the echinoid, *Echinocrinus*, occur with the corals. Crinoid ossicles, although tremendously abundant in many other beds, are not common in the coralline beds proper.

The corals themselves may be conspicuously abundant, as in zones 1 and 2, where they approach the nature of biostromes. Specimens of the colonial corals range in diameter from an inch or two up to elongate colonies eight feet long and a foot or two in height. Most colonies are from six inches to a foot in diameter. Specimens are infiltrated and replaced by calcite in all cases, whereupon they appear as white masses against the grey matrix of the limestone bed. Surficial silicification has affected some colonies so that the nature of the calices is revealed and the axial structures can be inspected with a hand lens in the field without resorting to preparation of thin sections or polished surfaces.

In many instances the colonies are planoconvex and lie in their positions of growth with the convex side up. In structurally complex areas, however, the entire stratigraphic sucession may be inverted, in which case the corals assist in determining the true orientation of the strata. At several localities there is abundant evidence of disruption of colonies by current action. Large colonies two or three feet in breadth are lying on their sides with fragments of the colonies strewn about in the matrix. Coralla with cylindrical corallites are naturally poorly compacted and are therefore particularly prone to be broken apart. Reworked colonies, of course, cannot be used for determination of stratigraphic tops, but the lineation of the fragments reveals the directions in which currents flowed.

STRATIGRAPHIC DISTRIBUTION

Zone 1 is commonly dominated by the presence of *Thysanophyllum princeps*. It has been found at essentially every outcrop of the basal Rib Hill limestone examined, and is particularly abundant in the eastern portion of the region. It occurs much less commonly in the lower limestone beds of the Arcturus formation. Here and there in zone 1 occur *Diphyphyllum connorsensis*, *Lithostrotionella dilatata*, and *Lonsdaleia cordillerensis*, particularly in the western portion of the region.

Zone 2 contains all seven species of corals described herein, but it is characterized by two species. *Caninia trojana* is confined to the top of zone 2 in east-central Nevada, although it seems to occur at a lower level (in the Wolfcamp Series) in the Spring Mountains of southern Nevada. The most conspicuous coral at most localities, however, is *Lonsdaleia cordillerensis*. Its fasciculate colonies may comprise most of the mass of many beds, and fragments of this species may occur in beds which seem to lack the corallites proper. The species also is present in limestone of Wolfcamp age in southeastern California. *Lithostrotionella dilatata* is also a rather common element in the lower Arcturus strata.

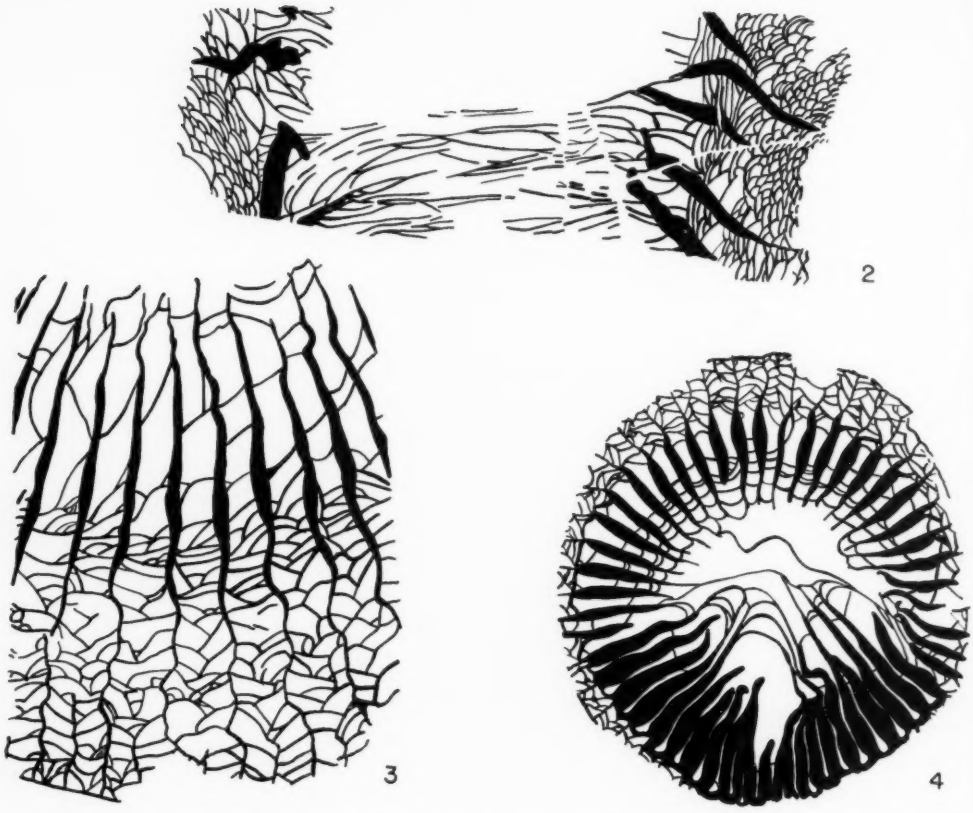
The upper cyclical limestone and sandstone sequence does not comprise a distinct faunal zone such as occurs in lower beds. Corals are less abundant than in lower strata and the fauna is more meager. *Lonsdaleia illipahensis* is rather consistently present in the sequence, although not strictly confined to it. The species is less common in the Arcturus formation. Specimens of *Lonsdaleia cordillerensis* which occur at a few places in the sequence seem to be a variety with unusually broad corallites.

The localities from which the corals were collected are described in a register appended to this report.

SYSTEMATIC DESCRIPTIONS

Phylum COELENTERATA
Class ANTHOZOA
Subclass RUGOSA
(TETRACORALLA)
Family CYATHOPSIDAE Dybowski, 1873
Genus CANINIA Michelin in Gervais, 1840

Diagnosis.—Caninia comprises solitary cyathopsids whose septa reach the center in early stages but retreat from the axis in



TEXT-FIGS. *2–4—Caninia trojana. 2*—longitudinal section of paratype in mature region, USC 5015, locality 330, ×1.3; *3*—Transverse section of late mature region, paratype, USC 5016, locality 330, ×4; *4*—Transverse section in early maturity, paratype, USC 5017, locality 330, ×1.3.

amplexoid fashion in maturity; septa normally are dilated in the tabularium; minor septa are short and are confined to the dissepimentarium; the cardinal fossula is distinct but the alar pseudofossulae are indistinct; the dissepimentarium is narrow to wide, mostly consisting of herringbone dissepiments between septa; lonsdaleoid dissepiments may be present near the periphery.

Remarks.—Caninia is particularly comcom in North America in Pennsylvanian strata. For instance, it occurs as minor biostromes in the Ely limestone of Nevada. The following species is noteworthy for its large diameter. It is the first species of *Caninia* described from the Permian of the Basin and Range Province. *Caninia* has also been referred to as *Campophyllum* and *Pseudozaphrentoides* in American literature.

CANINIA TROJANA n. sp.
Text-figs. 2–4

Exteriors.—Corals are simple, very large, curved, and have an apical angle of about 50°. The theca is very thin and either is smooth or bears faint septal grooves. The calyx is deep and is essentially flat-floored. The holotype, which is the largest relatively complete specimen, is 12 cm. long and is 9 cm. in diameter at the widest place; if this specimen were complete it would be about 15 cm. long. The deep axial portion of the calyx is about one-third as wide as the diameter of the coral. The cardinal fossula is on the concave side of the coral.

Transverse sections.—At the earliest observed stage of one specimen (diameter about 17 mm.) there are about 36 long major septa which are dilated until they essentially close off the intervening loculi and come within 2 or 3 mm. of meeting at the axis. About 5 major septa lie in each cardinal quadrant. Minor septa are not present. Possibly one rank of dissepiments is present. At a slightly later stage of the same specimen (diameter about 20 mm.) 2 or 3 ranks of herringbone dissepiments are present in a few loculi but minor septa are not present.

In early maturity (diameter 43 mm.) about 50 dilated major septa extend to within 5 mm. of the axis. Approximately 8 or 9 major septa lie in each cardinal quadrant. The short cardinal septum occupies a conspicuous fossula. Alar pseudofossulae are indistinct. Minor septa are absent. A dissepimentarium of 3 or 4 ranks of herringbone dissepiments is as much as 4 mm. wide and is broadest on the counter side of the coral. Loculi are not closed off by dilation of septa.

It is estimated that in late maturity (diameter about 90 mm.) 70 major septa are present in the holotype, of which possibly 10 may lie in each cardinal quadrant. Septa are less dilated than in earlier stages and they leave an open space on the tabularium about 25 mm. in diameter. The dissepimentarium is as broad as 15 mm., which is half the length of the septa. Dissepiments are almost entirely herringbone, except in the outer edges at a few places where slender minor septa up to 5 mm. in length are present; whereupon a concentric pattern is assumed by dissepiments. From 18 to 20 ranks of dissepiments may be present.

Longitudinal sections.—Apical regions are devoid of dissepiments but the dissepimentarium appears shortly and widens distally. Long axes of dissepiments lie essentially vertically or are inclined apically and inwardly as much as 15°. Dissepiments are mostly 2 or 3 mm. long, but here and there one attains a length of 5 mm. From 10 to 12 incomplete tabulae occur in 10 mm. in mature regions where they may be slightly concave axially. In youthful stages where the dissepimentarium is thin to lacking, only 4 or 5 tabulae are present in 10 mm. Tabulae near the periphery slope outward and apically. Tabulae in the axial region of adult specimens are essentially horizontal and are slightly more numerous than in youthful stages.

Comparison.—*Caninia trojana* is distinctly the broadest caninoid coral yet discovered in North America, and possibly is the broadest known to science. Some phases of *Caninia torquia* from the Pennsylvanian of Illinois approach 60 cm. (2 feet) in length, but the broadest specimen there measured only 5.2 cm. (Easton, 1944, p. 127).

Caninia trojana is larger than typical *C. torquia*, has more major septa in maturity, has less well developed minor septa, and has a less well developed dissepimentarium which is not introduced until late in the ontogeny.

Another unusually large caninoid is the Upper Mississippian species, *Caninia nevadensis* (Meek, 1877) from the Brazer formation of Stansbury Island in Great Salt Lake and from the Chainman shale of the Confusion Range, both localities being in Utah. Specimens with about 70 long septa attain a breadth of 7.5 cm. and may have been 25 cm. in length, if they were complete. *C. nevadensis* is essentially cylindrical instead of flaring.

Although caninoid corals occur locally in Late Paleozoic deposits in the Cordilleran region, the other species are all more cylindrical than flaring, and are less broad than *C. trojana*.

Occurrence.—USC localities 330 (type locality), 331, 346, 348, 349.

Material.—Holotype, USC 5104. Paratypes, USC 5105-5110. Topotypes, USC 5111. Other specimens, USC 5131, 5132, 5134, 5137. Collection contains 33 specimens.

Remarks.—Some of the herringbone dissepiments present in *C. trojana* differ somewhat from typical herringbone dissepiments because the present ones commonly consist of a transverse plate like a concentric dissepiment, against which two oblique plates abut across the outer angles.

Strata containing *C. trojana* in White Pine County lie near the base of the *Parafusulina* zone of Leonard fusulinids, whereas strata with *C. trojana* in the Spring Mountains contain Wolfcamp fusulinids.

Family LITHOSTROTIONIDAE
d'Orbigny, 1851

Diagnosis.—Compound rugose corals with the inner end of the counter septum functioning as an axial plate, but axial structures may be lacking in some strains. The dissepimentarium is lonsdaleoid in some groups.

Remarks.—McLaren & Sutherland (1949) have indicated that several genomorphs of *Lithostrotion* can be differentiated on the basis of variation in strength of axial structures, circular or prismatic corallites, and presence or absence of lonsdaleoid dissepiments. Their system is followed in part herein and genomorphs of *Lithostrotion* are indicated by brackets.

LITHOSTROTION [THYSANOPHYLLUM]
PRINCEPS n. sp.
Text-figs. 5,6

Exteriors.—Coralla are composed of prismatic corallites which are mostly 6 mm. in diameter. Coralla commonly attain diameters of 10 to 15 cm. but one mass 240 cm. in length and 20 cm. thick was observed in an outcrop. Calices are rather deep. Calical floors are almost flat or are gently convex.

Transverse section.—Corallites are irregularly polygonal and are separated by ungrooved thecae whose plane of juncture is denoted by a dark line. From 14 to 16 major septa extend across ⅓ of the radius. Minor septa, when present, commonly are merely short spines which scarcely penetrate one rank of dissepiments. Dissepimentaria commonly are composed of no more than 3 ranks of dissepiments. Marginal dissepiments commonly are lonsdaleoid but are not consistently of that pattern. Inner dissepiments and some marginal dissepiments are almost all concentric. Very few herringbone dissepiments are present. The tabularium is devoid of axial structures in most instances, but in a few sections there are isolated segments which might be either broken tabulae or median plates.

Longitudinal section.—The theca is only slightly contorted. Dissepiments are consistently globose and seem mostly to comprise one vertical series in which 12 dissepiments occur in 1 cm. Tabulae are mostly complete and are broadly arched distally. About 17 tabulae occur in 1 cm. No trace of an axial plate was observed.

Comparison.—*Lithostrotion* [*Thysanophyllum*] *princeps* differs from *Thysanophyllum orientale* (Thomson, 1876), from the Lower Carboniferous of Europe in having narrower corallites, about half as many septa, less well developed lonsdaleoid dissepiments, and in having more closely spaced tabulae.

The dissepimentarium of *Thysanophyllum princeps* resembles that of *Lonsdaleia illipahensis*, but *Thysanophyllum princeps* does not have an axial complex. *Lithostrotionella mokomokensis* has merely an axial plate for a columella, which might not be present in some sections, but *L. mokomokensis* has much coarser lonsdaleoid dissepiments than *T. princeps* has.

Occurrence.—USC localities 334 (type locality), 330, 335, 340, 341, 345, 348, 352, 360.

Material.—Holotype, USC 5112. Other specimens, USC 5113–5116, 5130, 5141, 5142, 5148. Collection contains 9 specimens.

Remarks.—Slight crushing of some specimens causes rupture and displacement of skeletal elements. Thus, isolated segments

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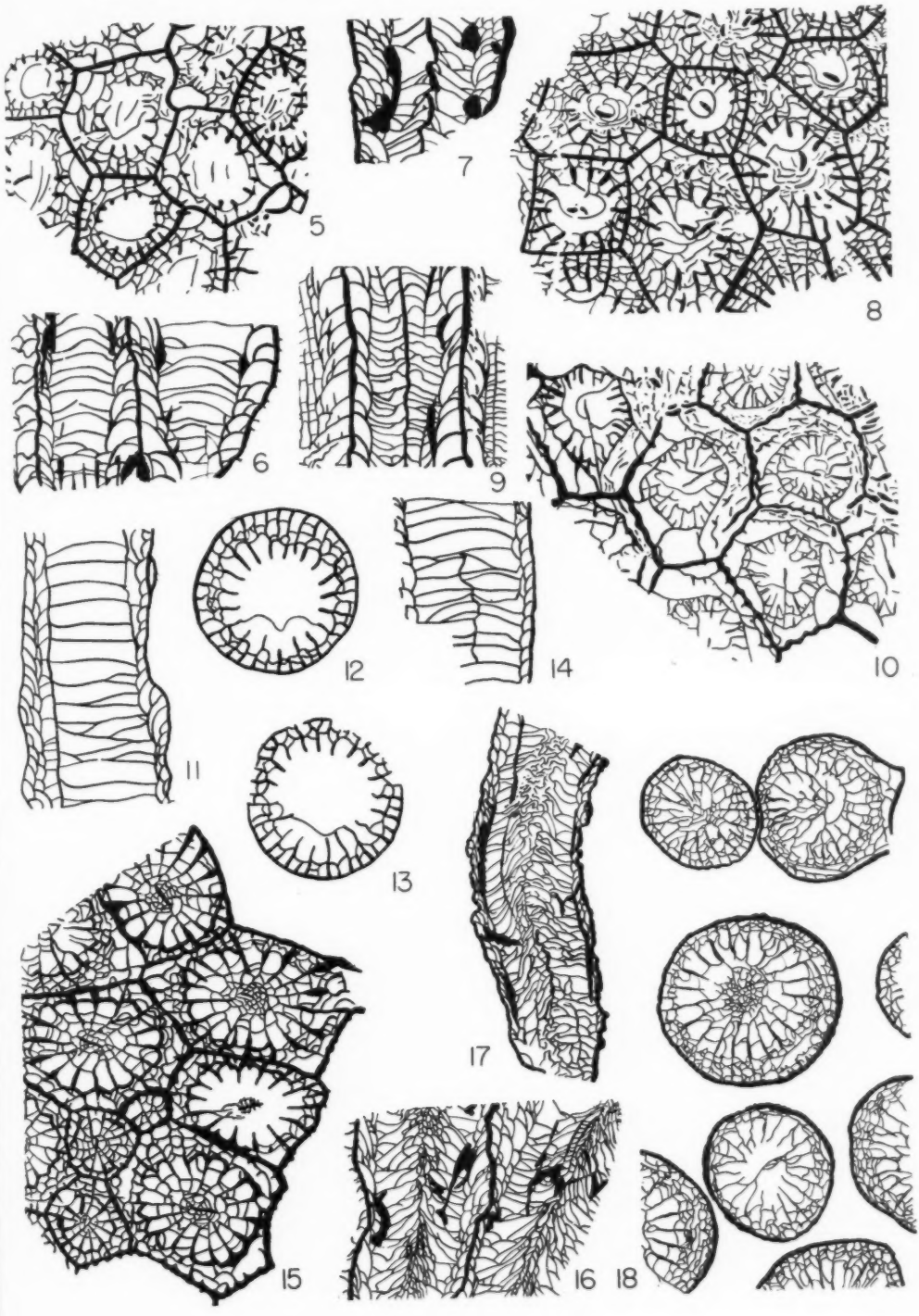
TEXT-FIGS. *5–18—5–6, Lithostrotion* [*Thysanophyllum*] *princeps.* Transverse and longitudinal sections, holotype, USC 5112, locality 334; *7,8, Lithostrotion* [*Lithostrotionella*] *dilatata.* Longitudinal and transverse sections, holotype, USC 5117, locality 340; *9,10, Lithostrotion* [*Lithostrotionella*] *mokomokensis.* Longitudinal and transverse sections, holotype, USC 5119, locality 330; *11–14, Lithostrotion* [*Diphyphyllum*] *connorsensis.* Longitudinal and transverse sections of four corallites, holotype, USC 5120, locality 332; *15,16, Lonsdaleia illipahensis. 15*—Transverse section, holotype, USC 5122, locality 336. *16*—Longitudinal section, a paratype, USC 5123, locality 337; *17,18, Lonsdaleia cordillerensis.* Longitudinal and transverse sections, holotype, USC 5127, locality 342. All figures ×3.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of tabulae in some corallites illustrated in text-figure 5 resemble the median plate of an axial structure.

LITHOSTROTION [LITHOSTROTIONELLA] MOKOMOKENSIS n. sp.
Text-figs. 9,10

Exteriors.—Corallum massive, sub-hemispherical to flattened, about 20 cm. in diameter (reconstructed) and at least 5 cm. thick. Mature corallites are mostly about 7 mm. in diameter and are 5- or 6-sided. The common wall between corallites projects above the conspicuously convex dissepiments in calices. Axial ends of septa penetrate the nearly vertically disposed inner slopes of dissepiments. Floors of calices are mostly domed and may retain the trace of the axial plate. Calices are 4 to 5 mm. deep.

Transverse sections.—Calical walls bear a distinct, median, dark line and commonly retain interseptal ridges. Calices are sharply divided into dissepimentaria and tabularia at a prominent inner wall. The dissepimentarium commonly consists of only 1 or 2 ranks of large, lonsdaleoid dissepiments which may be surmounted by few to many septal spines. The tabularium is subrounded to irregularly polygonal. Mature calices mostly contain 15 thin major septa, of which only one (the presumed counter septum) reaches and even slightly passes the axis. The axial end of the long septum is not dilated. Minor septa are present alternately with the majors but only extend half as far across the tabularium as the majors do.

Longitudinal section.—A single row of large, globose dissepiments normally lines each side of the tabularium. About 10 dissepiments occur in 1 cm. The tabularium is divided in half by the somewhat sinuous axial plate. Complete and incomplete tabulae are both present, there being from 15 to 20 in 1 cm. Tabulae rise slightly at the periphery to meet the dissepiments.

Comparison.—The best known clisiophylloids from North America are species of *Lithostrotionella* from the Mississippian System. *L. mokomokensis* resembles *L. tubifera* Hayasaka, 1936 from Montana in size of corallites, number of septa, and distinction between tabularium and dissepimentarium, but lacks the prominent ring-like juncture of septa with steeply-inclined tabulae which Hayasaka likened to a tube.

L. mokomokensis seems to be related to *L. berthiaumi* Merriam, 1942 from the Permian of Oregon. Both species have unusually large dissepiments, but *L. berthiaumi* has concave tabulae, more septa, and a stronger axial structure.

Occurrence.—USC localities 330 (type locality), 347, 349.

Material.—Holotype, USC 5119. Other specimens, USC 5133, 5136. Collection contains 3 specimens.

Remarks.—Although *Lithostrotionella* is confined to rocks of Meramec (Middle Mississippian) age in the midcontinent, it occurs from Mississippian into Permian strata in the Cordilleran region. Thin sections commonly are required in order to differentiate the various species. As a rule of thumb the Mississippian species seem to have rather more distinctly developed minor septa than are present among the Permian species.

LITHOSTROTION [LITHOSTROTIONELLA] DILATATA n. sp.
Text-figs. 7,8

Exteriors.—Coralla at least 15 cm. in diameter, rather spherical, and composed of prismatic corallites. Calices moderately deep and floored by a convex tabula from which projects a short but prominent axial plate.

Transverse sections.—Thecae smooth and separated one from another by a dark central line. About 16 or 17 major septa extend $\frac{2}{3}$ of the radius and are thickened within the tabularium. Minor septa are inconspicuous spines or septal crests near the periphery. Dissepimentarium consists of 1 to 5 ranges of mostly irregular concentric and herringbone dissepiments. A few lonsdaleoid dissepiments occur, particularly in recesses formed in the angles of the polygonal corallites. Columella consists of a single, slightly dilated plate. Elliptical outlines of tabulae surround the axial plate.

Longitudinal sections.—Thecae are slightly contorted. Dissepiments are somewhat elongate and slope inward at about 40°. About 20 dissepiments occur in 1 cm. along the theca. Tabulae are arched distally

at about 30° to meet the sinuous axial plate. From 14 to 18 tabulae occur in 1 cm. in the outer portion of the tabularium.

Comparison.—*Lithostrotion* [*Lithostrotionella*] *dilatata* differs from *L. mokomokensis* in having only sparse lonsdaleoid dissepiments, dilated major septa, and in having a dilated axial plate which is separate from the counter septum. Dissepimentaria of *Thysanophyllum princeps* and *Lonsdaleia illipahensis* are constructed similar to those of *L. dilatata*, but *T. princeps* lacks all trace of axial structure, and *L. illipahensis* has an arachnoid columella. All of the foregoing species construct coralla of prismatic corallites, hence they resemble each other at first glance.

Occurrence.—USC localities 340 (type locality), 345, 349–351, 332.

Material.—Holotype, USC 5117, Paratype, USC 5118. Other specimens, USC 5138–5140, 5149. Collection contains 6 specimens.

Remarks.—Assignment of this species to a genus raises questions which need to be investigated much more than in this introductory study. *Lithostrotionella dilatata* can be interpreted as a relative of *Lithostrotion* [*Thysanophyllum*] *princeps* which retains its axial plate, or it can be interpreted as a relative of *Lithostrotionella mokomokensis* which retains a simple dissepimentarium but has dilated septa and a dilated axial plate. Inasmuch as assignments are made herein on purely morphologic features, this species is referred at this time to the genomorph *Lithostrotionella*.

LITHOSTROTION [DIPHYPHYLLUM] CONNORSENSIS n. sp.
Text-figs. 11–14

Exteriors.—Coralla composed of loosely fasciculate corallites from 8 to 10 mm. in diameter. Coralla range up to at least 15 cm. in diameter. Corallites are cylindrical. Thecae bear faint septal grooves.

Transverse sections.—The theca is very thin. From 18 to 20 thin major septa extend up to ½ the radius. Short minor septa can be distinguished between some major septa. The dissepimentarium consists of 1 to 3 ranks of mostly concentric dissepiments.

Longitudinal sections.—The theca is locally wrinkled. Dissepiments are mostly rather globose, although a few elongate ones may be present. From 12 to 15 of the globose disseopients occur in 1 cm. Tabulae are thin, very slightly convex distally, and are complete (with rare exceptions). About 11 tabulae occur in 1 cm.

In one section (text-fig. 14) an axial plate can be traced over a sinuous course for 6 mm.

Comparison.—*Lithostrotion* [*Diphyphyllum*] *connorsensis* resembles *Lonsdaleia cordillerensis* in being composed of loosely fasciculate corallites, but *L. connorsensis* lacks an axial structure. *L. connorsensis* resembles corals of similar form in the Monte Cristo formation (Mississippian) of the Basin and Range Province which seem to be referable to *Lithostrotion* [*Siphonodendron*] sp. (Easton, 1957, p. 619), but the Mississippian coral normally retains its axial plate and tent-like tabulae, whereas *L. connorsensis* normally lacks an axial plate and has simply-arched tabulae.

Occurrence.—USC localities 332 (type locality), 334, 349, 355, 357.

Material.—Holotype, USC 5120. Other specimens, USC 5121, 5135, 5143, 5145. Collection contains 5 specimens.

Family LONSDALEIIDAE Chapman 1893
Genus LONSDALEIA M'Coy, 1849

Diagnosis.—Mostly compound corals with arachnoid columellae, major and minor septa, one order of essentially transverse tabulae, and an outer zone of lonsdaleoid dissepiments.

Remarks.—Hudson (1958, p. 178) has commented on the recent tendency to assign *Lonsdaleia*-like Permian corals to genera such as *Waagenophyllum* and *Wentzelella*. These genera have transverse inner tabulae but have steeply-inclined outer tabulae (clinotabulae), and some of them have a tertiary order of septa. The material at hand, however, seems to represent the orthodox morphology of *Lonsdaleia*. Inasmuch as *Waagenophyllum* is definitely known from Cordilleran deposits through the researches of Smith (1935) and Merriam (1942), it is possible that the genus will be discovered among the rich coral faunas of the eastern part of the Basin and Range Province.

LONSDALEIA ILLIPAHENSIS n. sp.
Text-figs. 15,16

Exteriors.—Coralla are composed of prismatic corallites which mostly are from 7 to 10 cm. in diameter and are depressed hemispherical. Calices are rather deep with sloping inner margins and a low, dome-shaped, axial boss on the calical floor.

Transverse sections.—Corallites are irregularly polygonal. Thecae have smooth margins and are joined along a dark median line. From 12 to 17 rather sinuous major septa traverse as much as $\frac{2}{3}$ of the radius of a mature corallite. Minor septa are present near the periphery but rarely traverse more than two ranks of dissepiments. The dissepimentarium occupies approximately $\frac{1}{3}$ of the radius. Outer dissepiments are irregularly concentric. Commonly 4 or 5 ranks of dissepiments are present. The axial structure is distinctly arachnoid and may occupy most of the tabularium. As many as 2 or 3 ranks of tabellae surround a slightly thickened median plate. Lamellae transect the tabellae and may correspond in number and position with the major septa; or lamellae may be reduced in number until they are almost lacking. Major septa may touch the axial structure at some points and may even be confluent with some lamellae.

Longitudinal section.—Thecae are somewhat sinuous. Dissepiments are rather elongate and occur in 1 to 3 ranks. About 12 to 14 dissepiments occur in 1 cm. Tabulae slope peripherally at only about 15° to 30°. Some incomplete tabulae are present and approximately 22 tabulae of both kinds occur in 1 cm. The axial complex is composed of closely-spaced tabellae which slope distally at very steep angles and may be vertical or even overhang slightly. The median plate is broadly sinuous, as are the lamellae.

Comparison.—*Lonsdaleia illipahensis* resembles species of *Lithostrotionella* from the Mississippian of North America which have prismatic corallites, but *L. illipahensis* has an arachnoid columella, whereas the columellar structure of *Lithostrotionella* consists merely of a median plate.

Lonsdaleia illipahensis resembles *Thysanophyllum princeps* externally, but has an arachnoid columella instead of no columella. *L. illipahensis* also resembles *Lithostrotionella mokomokensis* externally, but has a more complicated columella and lacks the broad lonsdaleoid dissepimentarium of the latter species.

Occurrence.—USC localities 336 (type locality), 332, 337–339, 359.

Material.—Holotype, USC 5122. Paratype, USC 5123. Other specimens, USC 5124–5126, 5147. Collection contains 6 specimens.

Remarks.—*Lonsdaleia illipahensis* varies somewhat in strength and number of major septa. A specimen from the lower part of the Arcturus formation has about 14 or 15 major septa and they mostly do not reach the axial complex. On the other hand, a specimen from the cyclical beds above the Arcturus formation has about 17 septa in each corallite, and the septa mostly reach the axial complex.

LONSDALEIA CORDILLERENSIS n. sp.
Text-figs. 17,18

Exteriors.—Coralla are composed of loosely fasciculate corallites about 10 to 12 mm. in diameter. Diameters of coralla range from about 10 cm. up to great masses which approach a meter in diameter. Calices are deep, lined with prominent septal ends, and are occupied by a very prominent axial boss on which traces of tabellae are preserved.

Transverse sections.—Mature calices of the holotype at a diameter of 9 mm. contain from 22 to 28 thin major septa, a few of which reach the axial structure. Most major septa reach the theca. Minor septa are inconspicuous and short; moreover, they may not be present in all quadrants. Dissepimentaria occupy as much as $\frac{1}{3}$ of the radius and consist of about 5 ranks of dissepiments when best developed. Dissepiments are mostly herringbone. Although a few lonsdaleoid dissepiments may be present at some positions in some calices, they are not consistently present.

The axial structure is a well-developed arachnoid columella which occupies almost the entire tabularium in its most highly developed condition. On the other hand, corallites of mature dimensions may bear only feebly developed columellae. Tabellae and lamellae are somewhat sinuous and irregularly disposed, thus rendering the

axial structure both complex and variable. Moreover, calices as much as 7 mm. in diameter and containing 20 major septa may lack all traces of a columella. The theca is thin and lacks distinct septal grooves.

Longitudinal section.—The theca is wrinkled conspicuously. Dissepiments are closely packed and of various shapes, but are mostly hemispherical. From 25 to 30 tabulae occur in 1 cm. and mostly slope away from the axial complex at 15° to 30°. The axial complex consists largely of tightly-packed, sinuous tabellae which slope away from the center at angles up to about 70°. The median plate is sinuous and thin, as are the traces of lamellae.

Comparison.—Lonsdaleia cordillerensis resembles species of *Waagenophyllum* such as *W. columbicum* Smith, 1935 in cylindrical shape of corallites and presence of an arachnoid columella, but *L. cordillerensis* has transverse tabulae instead of some transverse tabulae and some clinotabulae.

L. cordillerensis also resembles species of *Waagenophyllum* described from the Permian of Oregon by Merriam (1942) in similar growth habit, but has lonsdaleoid dissepiments and lacks clinotabulae.

Diphyphyllum connorsensis also has cylindrical corallites, but it generally is devoid of any axial structure.

Occurrence.—USC localities 342 (type locality), 332, 343, 344, 356, 358, 360.

Material.—Holotype, USC 5127. Other specimens, USC 5128, 5129, 5144, 5146, 5150, 5151. Collection contains 7 specimens.

Remarks.—This species is referable to *Lonsdaleia* with doubt in some instances because corallites seem to lack the characteristic lonsdaleoid dissepiments. On the other hand, clinotabulae are not present so it can scarcely be referred to *Waagenophyllum*.

In its typical occurrence the corallites are only about 8 mm. in diameter, but in the cyclical sediments overlying the Arcturus formation the corallites attain diameters of perhaps 15 mm. Perhaps it will be advisable to differentiate these varieties in future studies.

LOCALITY REGISTER

USC 330. Buff, fine-grained, silty, thick-bedded limestone in the lower part of the Arcturus formation. Outcrops extend north-south along the synclinal crest of Mokomoke Ridge in the southwest part of the Illipah quadrangle, Nevada, along a line about 500 feet west of the centers of sec. 4, T. 16 N., R. 58 E., and sec. 33, T. 17 N., R. 58 E. The ridge crest can be reached by a rough vehicle trail which ascends the south end of Mokomoke Ridge northward from a point on the gravel road about 1 mile east of Hamilton.

USC 331. Grey, massive limestone of the Bird Spring formation along the crest of the ridge which strikes N. 55° E. and lies 6 miles S. 80° W. from the intersection of Lee Canyon (Nevada Highway 52) and the Indian Springs road (U. S. Highway 95) about 27 miles northwest of Las Vegas, Clark County, Nevada. The locality can be reached by driving 2.5 miles cross-country up the alluvial fan southwest from U. S. Highway 95. The locality lies 2300 feet stratigraphically above the contact of the Bird Spring formation upon the Monte Cristo formation (Mississippian). This zone is at the base of the Permian System (Wolfcamp) in the section referred to by Longwell and Dunbar (1936).

USC 332. Base of 125 foot dark grey limestone comprising the lower part of the Arcturus formation. Outcrops form prominent, partly overhanging bluff and road cut on the north side of former U. S. Highway 93, about 1.2 miles east of the summit of Connors Pass and about 23 miles southeast of Ely, Nevada. Probably near SE cor., sec. 26, T. 14 N., R. 65 E.

USC 333. Light grey, sandy, buff-weathering limestone in the lower part of the Arcturus formation. Outcrops are located on the west side of U. S. Highway 6, about 3 miles SW of Ely, Nevada. Sec. 25, T. 16 N., R. 62 E., Ely quadrangle.

USC 334. Buff limestone at the base of the Rib Hill formation, forming bluff about 200 yards north of U. S. Highway 50 at a point 1 mile east of the Hamilton road. Near cen., sec. 7, T. 17 N., R. 59 E., Illipah quadrangle.

USC 335. Grey limestone 140 feet thick, lying 40 feet stratigraphically below sandstone beds of the Rib Hill formation, due west of 2 large water tanks at the SE end of the north ridge of Rib Hill, 1 mile SW of

Ruth, Nevada. Near SE cor., sec. 16, T. 16 N., R. 62 E., Ely quadrangle.

USC 336. Bluff of brown limestone overlying white limestone on north side of dry valley where unimproved road crosses creek bed, 1.1 miles west of Ruby Valley Truck Trail (Ruby Marsh Road) and 6 miles north of U. S. Highway 50. SE, SW, SW, sec. 8, T. 18 N., R. 59 E., Illipah quadrangle.

USC 337. Grey limestone cropping out 2200 feet along forest road running northwest of Murry Summit about 6 miles southwest of Ely, Nevada. Cen., S½, sec. 27, T. 16 N., R. 62 E., Ely quadrangle.

USC 338. Buff limestone 300 feet stratigraphically above the base of measured section 2 published by Knight (1956, p. 776). About 600 feet above U. S. Highway 50, on north side of road, about 0.3 mile west of Moorman Ranch. Cen., E½, NW, sec. 9, T. 17 N., R. 59 E., Illipah quadrangle.

USC 339. Grey limestone 13 feet thick cropping out in road cut on the north side of U. S. Highway 6, 200 yards west of Murry Summit, about 6 miles southwest of Ely, Nevada. NE, NE, NE, sec. 34, T. 16 N., R. 62 E., Ely quadrangle.

USC 340. Upper 10 feet of 125 foot bluff of limestone at locality 332.

USC 341. Prominent outcrop of biostromal limestone alongside the rough road through Indian Pass, Confusion Range, Utah. Outcrops are probably in the Arcturus formation. Locality is 1400 feet NW of benchmark 5970.

USC 342. Bluff of coralline limestone on the low spur extending southwest from the prominent hogback on the south side of Rib Hill, about 2 miles south of Ruth, Nevada. Basal limestone of the Arcturus formation. Cen., SW, sec. 22, T. 16 N., R. 22 E., Ely quadrangle. Can be reached on faint vehicle trails leading southwest from the main road into the center valley of Rib Hill.

USC 343. Grey, cherty, bluff-forming limestone 7 feet thick, a short distance up hill from locality 335 but 70 feet stratigraphically below that locality. Basal limestones of probable Wolfcamp age beneath the main sandstone body of the Rib Hill formation.

USC 344. Low bluff of limestone overlying light grey dolomite. On the east face of the Providence Mountains at the juncture of two prominent spurs due west of the Gilroy Mine, San Bernardino County, California. Locality is about ½ mile north of Mitchell's Caverns.

USC 345. Same limestone described in locality 332, but comprising a faulted extension to the north but offset about 500 feet westward and cropping out on the north side of old U. S. Highway 93.

USC 346. Prominent bluff of limestone along the southwest face of the hills north of the deep canyon draining westward in the NE, SE, sec. 12, T. 18 N., R. 57 E., Illipah quadrangle. Can be reached from roads in the Pancake Summit quadrangle. Basal limestone of the Arcturus formation.

USC 347. From steep slope of limestone about 20 feet above the rim of the prominent bluff described in USC 346.

USC 348. Rounded slopes developed on the basal limestone of the Arcturus formation in the cen., E½, NE, sec. 3, T. 19 N., R. 57 E., Buck Mountain quadrangle.

USC 349. Prominent bluff of limestone in the lower part of the Arcturus formation cut by Circle Wash about 100 feet south of the road and down the slope from benchmark 7633. Near NW, sec. 33, T. 15 N., R. 59 E., Treasure Hill quadrangle.

USC 350. Limestone bluff in the lower part of the Arcturus formation where Circle Wash cuts southeastward through the hills about 200 yards south of Circle Wash reservoir. Probably cen., W½, sec. 26, T. 15 N., R. 59 E., Treasure Hill quadrangle.

USC 351. Steeply west-dipping limestones about 100 yards east of Circle Wash Road in a V-shaped gully with dry falls of bold outcrops. Probably sec. 22, T. 15 N., R. 59 E., Treasure Hill quadrangle. Basal limestones of the Rib Hill formation.

USC 352. Low ridge of Arcturus limestone about ½ mile west of USC 349 and on the west side of the road south from benchmark 7633. W line, sec. 33, T. 15 N., R. 59 E., Treasure Hill quadrangle.

USC 355. Basal limestone of the Arcturus

formation on a prominent shoulder on the inverted mountain at a point 2100 feet south and 2850 feet east of NW corner of Illipah #1 (SE) advance sheet.

USC 356. From third distinctly resistant limestone about 275 feet stratigraphically above the base of the Arcturus formation on the west face of the inverted mountain. 2800 feet south and 2450 feet east of NW corner of Illipah #1 (SE) advance sheet.

USC 357. Limestone at the base of the Rib Hill formation on a prominent shoulder on the west side of the inverted mountain. 1200 feet due east of hill 8028 on Illipah #1 (SE) advance sheet.

USC 358. From lower massive limestone of cyclical beds overlying the Arcturus formation on the first knoll at the south end of the SW-trending low ridge at a point 7450 feet west and 3800 feet north of the SE corner of Illipah #1 (SW) advance sheet. Easily reached by old road SE from Moorman Ranch across Jake's Valley, then south along base of hills and up the slope on an old sheep camp trail.

USC 359. From massive, grey, coralline limestone at the base of the Arcturus formation on a ridge crest about 100 feet south of a small but very prominent outcrop on a knoll 5700 feet west and 9650 feet north of the SE corner of Illipah #1 (SW) advance sheet.

USC 360. Bluff of limestone (strike 078, dip 25 SE) lying about 50 feet down the north face of the knoll half a mile south of U. S. Highway 93, in NW, NW, sec. 36, T. 14 N., R. 65 E., Ely quadrangle. This is the lower limestone of the Arcturus formation and is the continuation a long strike southward from USC 332.

LITERATURE CITED

EASTON, W. H., 1944, Revision of Campophyllum in North America: Jour. Paleontology, v. 18, no. 2, p. 119–132, pl. 22, 4 text-figs.

——, 1957, On the tetracoral *Lithostrotion harmodites* Milne-Edwards and Haime: *ibid.*, v. 31, no. 3, p. 616–622, pl. 71.

EHRING, T. W., 1957, The Murry Formation (Permian) Nevada: Thesis, Master of Art (Geology), University of Southern California, Los Angeles, California, 47 p., 4 pls.

HAYASAKA, ICHIRO, 1936, On some North American species of Lithostrotionella: Mem. Faculty Science Agriculture, Taihoku Imp. Univ., v. 13, no. 5, p. 47–73, pl. 11–17.

HUDSON, R. G. S., 1958, Permian corals from northern Iraq: Paleontology, v. 1, pt. 3, p. 174–192, pls. 32–35, 4 text-figs.

KNIGHT, R. L., 1956, Permian fusulines from Nevada: Jour. Paleontology, v. 30, no. 4, p. 773–792, pls. 83–88, 3 text-figs.

LANGENHEIM, R. L., and MCCUTCHEON, V. A., 1959, *Bayhaium merriamorum*, a new Permian tabulate coral from California: *Ibid.*, v. 33, no. 1, p. 99–102, pl. 19.

LONGWELL, C. R., & DUNBAR, C. O., 1936, Problems of the Pennsylvanian-Permian boundary in southern Nevada: Am. Assoc. Petroleum Geologists, v. 20, no. 9, p. 1198–1207.

MCLAREN, D. J., & SUTHERLAND, P. K. 1949, *Lithostrotion* from northeast British Columbia and its bearing on the genomorph concept: Jour. Paleontology, v. 23, no. 6, p. 625–634, pl. 103, 4 text-figs.

MERRIAM, C. W., 1942, Carboniferous and Permian corals from central Oregon: *Ibid.*, v. 16, no. 3, p. 372–381, pls. 54–57.

MOORE, R. C., & JEFFORDS, R. M., 1941, New Permian corals from Kansas, Oklahoma, and Texas: Kansas Geol. Survey Bull. 38, pt. 3, p. 65–120, pls. 1–8.

SMITH, STANLEY, 1935, Two Anthrocolithic corals from British Columbia and related species from the Tethys: Jour. Paleontology, v. 9, no. 1, p. 30–42, pls. 8,9.

THOMPSON, M. L., & HAZZARD, J. C., 1946, Permian fusulinids of southern California: Geol. Soc. Amer., Mem. 17, p. 37–53, pls. 10–18, 4 text-figs.

JOURNAL OF PALEONTOLOGY, V. 34, NO. 3, P. 584–588, 1 TEXT-FIG., MAY, 1960

THE TYPE LOCALITIES OF THE MAESTRICHTIAN (MAESTRICHTIAN CHALK TUFF) AND OF THE MONTIAN (TUFFEAU DE CIPLY, CALCAIRE DE MONS, LAGUNAR, AND LACUSTRE MONTIAN)

J. HOFKER
The Hague, Netherlands

ABSTRACT—A recent paper by Loeblich & Tappan induced the author to give an account of our recent knowledge about the Maestrichtian-Montian sequence in Holland and Belgium, where these strata were described for the first time. There is considerable doubt as to the correlation of Danian and Paleocene, and the question is discussed whether the so-called planktonic faunal break of Foraminifera is a time-line. Contrarily to Loeblich & Tappan, the author concludes that at least at the type locality of the Maestrichtian of Dumont, the Maestrichtian Chalk Tuff, this faunal break is found not above but below this zone, at the boundary between the Gulpen Chalk and the Tuff. Moreover, the Tuffeau de Ciply, the lower Montian of Dewalque, is not the oldest known Paleocene in Holland and Belgium.

INTRODUCTION

A RECENT paper in this Journal by Loeblich & Tappan (1957, p. 1109–1138) clearly shows that the sequence of formations which in Europe are known as Maestrichtian and Paleocene often is misunderstood by American geologists, and it seems to be wise to give here a short account of our knowledge of the stratigraphy of the Maestrichtian and Paleocene in Holland and Belgium, from where the names "Maestrichtian" and "Montian" were derived.

Dumont was the first to use the term "Maestrichtian" for formations better known here as the "Maestrichtian Chalk Tuff" from the neighborhood of Maestricht, Holland. Dewalque was the first to propose the term "Montian" in southwestern Belgium. Nowadays it has become common usage to define the base of the Maestrichtian stratum much lower than was first proposed by Dumont, and to identify the base of the Maestrichtian with the first appearance of the *Belemnella lanceolata* group in Europe and elsewhere. In my publications I have always considered this lower boundary to be Campanian-Maestrichtian in the sense of Grossouvre. Hence the stratigraphy discussed by Loeblich & Tappan (1957, p. 1115 and 1116) seems confused. Lower Maestrichtian in European international sense is the *B. lanceolata* zone, whereas Ma–Mb already is the upper junior zone, with at least 4 or 5 stages between them!

In Holland and Belgium, thick sections, many with remarkably complete sequences, have been thoroughly sampled by the author and his collaborators. Whereas in Belgium gaps occur in the sequence, as I stated in another paper, from some drillholes in Holland very fine and nearly continuous sections have been obtained, extending through the Cretaceous-Tertiary boundary. These thousands of samples reveal the true position of the different zones, and Foraminifera occurring in the various zones have been analysed. Some species which seemed to be of more outstanding stratigraphic or biological value have already been described in my preliminary publications, and a few of them were quoted in the paper by Loeblich & Tappan. My final paper is finished.

It will be of some interest to give here the sequence of formations as they have been found in Holland and Belgium. The zone here called Me consists of an uppermost zone of Maestrichtian Chalk Tuff, in which glauconite is abundant (in contrast to the real Chalk Tuff) and contains a foraminiferal fauna with many transitional forms between those found in the Md and those found in the overlying "Lower Paleocene." This latter formation, given here as "Lower Paleocene," mainly contains the same fauna that Brotzen found in his "Paleocene" of Sweden, which is stratigraphically

younger than the type Danian. The fauna supports his conclusion, contrary to the suggestion by Loeblich & Tappan. In Holland this formation is found overlying the uppermost Md, or the Me, or the Kunrade chalk, in different localities. In the Basin of Mons in Southern Belgium, this lower Paleocene is found in hollows in the basal hard ground or basal conglomerate of the Tuffeau de Ciply (Poudingue de la Malogne). In the Dutch drill holes and mine shafts in southern Limburg, the formation covering the "Lower Paleocene" is lithologically as well as paleontologically identical with the "Tuffeau de Ciply," the lower part of the typical "Montian." This Tuffeau de Ciply in Holland is covered by typical Calcaire de Mons identical with that of the type-locality, the drill hole Goffint near Mons, Belgium. Over that formation lies the lagunar Montian which contains the fauna described by Haymes from the Thanetian of southern England. So, it seems to the author, that the identification by Loeblich & Tappan of Danian, Midway (Lower Paleocene), Montian, and Thanetian is rather premature. Stratigraphers and paleontologists here in Europe are working hard on these problems. They have not yet reached the conclusions attained by Loeblich & Tappan, and are not sure that they will come to similar conclusions as yet.

Recent investigations by the author proved that the type Montian does not contain *Globigerina daubjergensis* Bronnimann, but instead numerous specimens of *Globorotalia pseudomenardii* Bolli and thus belongs to a much younger Paleocene age than suggested by Loeblich & Tappen.

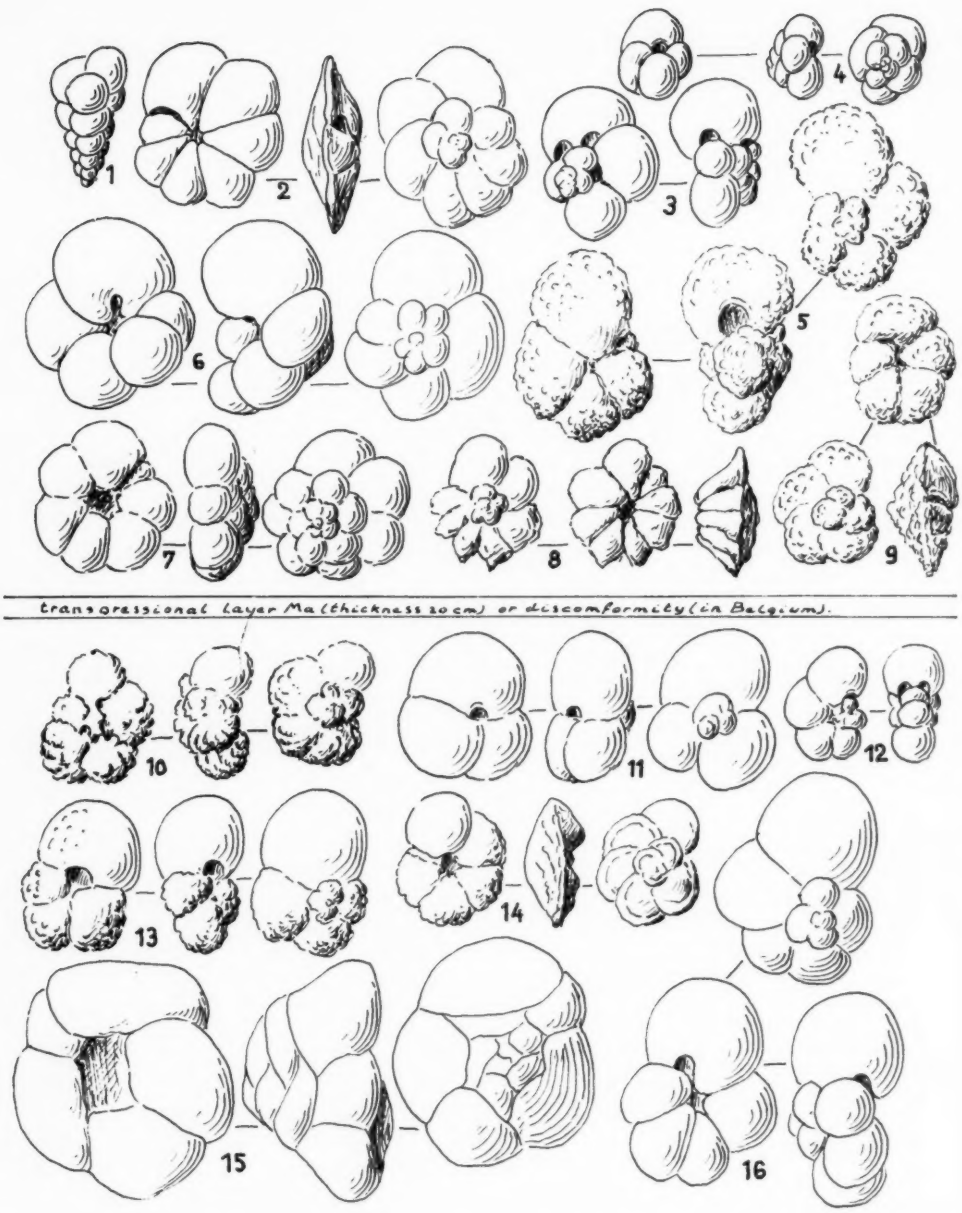
The author paid particular attention to what is known as the faunal break of the Cretaceous-Tertiary boundary. In the numerous series of samples, containing thousands of specimens, I did not find real Cretaceous planktonic genera such as *Rugoglobigerina* and *Globotruncana* in the Maestrichtian Chalk Tuff above the Ma, such as Loeblich & Tappan report. Only scattered specimens of these genera, all certainly reworked and extremely rare, were found in the basal conglomerates between the different sub-zones of that formation and in these zones all indications of small transgressional movements were found together with many benthonic reworked specimens. On the other hand, in many samples obtained from Mc and Md, abundant planktonic globigerines and rare *Globorotalia* were found, all of the Dano-Montian type as described from other regions. This would indicate, that, at least in the type-locality of the "Maestrichtian" (s.s. of Dumont), the faunal break is found not above, but below this formation. This could be more fully established in a fine series of samples, going through the Cr 4 and Lower Mb, where, just at the Maestrichtian Chalk Tuff *Globotruncana* and *Rugoglobigerina* disappear, and the globigerines with Tertiary aspect and the first *Globorotalia* appear. This would make it seem that this faunal break does not always indicate the Cretaceous-Tertiary boundary, for, as quoted by Loeblich & Tappan, mosasaurs, rudists, belemnites, and real ammonites continue in the sub-zones Mb–Md (not in the Me above). But we have to bear in mind that, in the Middle East, for example, ammonites and other Cretaceous guide fossils have already disappeared far below that faunal break. So several questions have been left open:

a. Is the faunal break a time-line?
b. Is the disappearance of ammonites and belemnites a time-line?
c. Are those time-lines, when they exist, identical or not?

These questions have not even been mentioned by Loeblich & Tappan. In the author's opinion they are of fundamental importance and have not been answered anywhere until now.

In text-figure 1, I figure only the commoner species of globigerines, *Globotruncana*, *Globorotalia*, and a *Gümbelitria*, occurring in the Cr 4 just below the Ma or the disconformity replacing this Ma, and those just above.

Those on the lower half of the text-figure thus occurring in the uppermost Gulpen chalk, and just below the "Maestrichtian" of Dumont, consist of species of the genera *Rugoglobigerina* and the latest known *Globotruncana*, together with species of *Globigerina* which do not show the *G. cretacea*-type, but that of species which generally are found just at the faunal break of the planktonic Foraminifera. Also, *Biglobigeri-*



TEXT-FIG. *1*—Upper Cretaceous and Paleocene Foraminifera. 1. *Gümbelitria mauriciana* Cole; boundary Mc–Md. 2. *Globorotalia membranacea* (Ehrenberg); Lower Md. 3. *Globigerinoides hyalina* Hofker; Upper Md. 4. *Globigerina compacta* Hofker; Upper Md and Lower Paleocene. 5. *Globigerina primitiva* Finlay; boundary Mc–Md. 6. *Globigerina* cf. *turgida* Finlay; boundary Mc–Md. 7. *Globigerina supracretacea* Hofker; Mb. 8. *Globorotalia praetuberculifera* Hofker; Mb. 9. *Globorotalia angulata* (White); boundary Mc–Md. 10. *Globigerina* (*Rugoglobigerina*) *rugosa* Plummer; upper Cr 4. 11. *Globogerina* sp.; upper Cr 4. 12. *Globigerina* (*Biglobigerinella*) *biforaminata* Hofker; upper Cr. 4. 13. *Globigerina* cf. *linaperta* Finlay; upper Cr 4. 14. *Globotruncana* cf. *esnehensis* Nakady; upper Cr 4. 15. *Globotruncana contusa* (Cushman); upper Cr 4. 16. *Globigerina* cf. *cretacea* d'Orbigny; upper Cr 4.

TABLE 1—SEQUENCE OF FORMATIONS FOUND IN SOUTH LIMBURG, NETHERLANDS

Stages	Zones and local groups of formations				Local names of formations	Belemnites zones (after F. Schmid)	Occurrences of planktonic genera	Transgressional disconformities or sedimental small gaps with sudden faunal changes
Paleocene		Montian	Thanetian or Upper Paleocene		Lagunar Montian	No Belemnites	Globigerines of the Lower Tertiary and *Globorotalia* Paleocene of Brotzen	←
			Lower Paleocene		Calcaire de Mons			←
					Tuffeau de Ciply			
					Lower Paleocene			←
Maestrichtian	Danian?	Maestrichtian Chalk Tuff (Maestrichtian s.s. of Dumont)		Kunrade Chalk	Me	*Belemnella casimirovensis*	No *Globotruncana* No *Rugoglobigerina* *Globorotalia* Globigerines of Tertiary types	
					Md			←
					Mc	*Belemnitella mucronata junior*		←
					M6			← Planktonic faunal break
		Chalk	Upper Maestrichtian		Cr4	Ma	*Globotruncana* *Rugoglobigerina*	
					Cr3c			
					Cr3γ		*Globotruncana* (*pauperata*)	←
			Lower Maestrichtian		yellow Cr3b	*Belemnella lancea lata*	*Globotruncana* and *Globigerina cretacea*	
					white Cr3b			←
Campanian		Gulpen	Upper Campanian		Cr3a	*Belemnitella mucronata senior*	hard ground *Globotruncana* and *Globigerina cretacea*	←
			Middle Campanian		Cr2 or Hervian	*Actinocamax quadratus* and *Belemnitella mucronata sen.*	unconformity *Globigerina cretacea*	

nella is present, which continues with higher specialised forms in the lower Mb. *Gümbelina* is not figured, since that group continues into the Eocene all over the world, and is easily transported by transgressional movements.

In the upper half of the text-figure are the common species of the Maestrichtian Chalk Tuff, the type-locality of the "Maestrichtian s.s" We find no *Globotruncana*, no *Rugoglobigerina*, and many species of globigerines (there are many more of those forms than I illustrated) all of the Tertiary type, as will be easily seen from text-figure 1. Moreover, there are several species of *Globorotalia*, some of them in special layers extremely common, which are not only of types of the *Truncorotalia*-type (*Globorotalia mosae* has not been figured, since it has been disputed by Loeblich & Tappan as

not belonging to *Globorotalia*), but also of keeled types. *Gümbelitria* is not, as stated by Loeblich & Tappan, of a Cretaceous type but of the type found in the Velasco, which is considered by Loeblich & Tappan as Paleocene. I figured also a specimen of my *Globigerina* (*Globigerinoides*) *hyalina*, in which also other dorsal sutural openings could be seen, thus proving that it cannot be a "malformed *Biglobigerinoides*."

There is, to my opinion, no doubt about the fact that the faunal break, considered by Loeblich & Tappan as the indicator of the Cretaceous-Tertiary boundary, is found not above, but below the "Maestrichtian Chalk Tuff" of Dumont.

Recent investigations by the author in Denmark proved that the boundary Skrivekridt-Danian in Denmark is identical in time with the boundary Upper Gulpenchalk-Maestrichtian Chalk Tuff in Holland; moreover the guide-fossil *Globigerina daubjergensis* shows at the top of the type-Danian just that stage of development as is found at the top of the Maestrichtian Chalk Tuff, the type of the "Maestrichtian" of Dumont. Several orthogeneses of Foraminifera common in the Maestrichtian Chalk Tuff of Holland and in the Danian of Denmark begin similarly in the base of both formations and end similarly at their top. This suggests that the Danian type-formation and the Maestrichtian type-formation are of the same age.

REFERENCES

HOFKER, J., 1955, Foraminifera from the Cretaceous of southern Limburg, Netherlands, VI, *Globorotalia* (*Truncorotalia*) *mosae* nov. sp.: Natuurhist. Maandblad, v. 44, p. 99–101, figs. 1,2.

——, 1956a, *Idem*, XIX, Planktonic Foraminifera of the Chalk Tuff of Maestricht and environments: *Ibid.*, v. 45, p. 51–7, figs. 1–24.

——, 1957a, *Idem*, XXV, Some more planktonic Foraminifera from the Lower Md in the quarry Curfs, Houthen: *Ibid.*, v. 46, p. 57, 58, figs. 1–9.

——, 1957b, *Idem*, XXVI, *Globorotalia praetuberculifera: Ibid.*, p. 59, 60.

——, 1958a, *Idem*, XXXIII, *Globigerina compressa* Plummer: *Ibid.*, v. 47, p. 42–44, figs. 1,2.

——, 1959a, *Idem*, XXXIX, Arguments for a Lower Paleocene age of the sediment above the upper Md in the quarry of Curfs near Houthen: *Ibid.*, v. 48, p. 18–30.

——, 1959b, *Idem*, XXXX, The age of the Cr 4'craie tuffoide: *Ibid.*, p. 46–53.

——, 1959c, *Idem*, XLII, On the development stage of *Globigerina pseudobulloides* Plummer in the Maestrichtian Chalk Tuff: *Ibid.*, p. 80–83.

——, 1959d, *Idem*, XLIII, Globigerines and related forms in the Cretaceous and Lower Paleocene of South Limburg: *Ibid.*, p. 89–95.

——, 1956b, Les Foraminifères de la zone de contact Maastrichtien-Campanien dans l'est de la Belgique et le Sud des Pays-Bas: Ann. Soc. géol. Belgique, v. 80, p. B191–233, figs. 1–79.

——, 1958b, Les Foraminifères du Crétacé supérieur de Glons: *Ibid.*, v. 81, p. B467–93, figs. 1–49.

———, 1960, The Foraminifera of the lower boundary of the Danish Danian: Med. Dansk Geol. Forening, v. 14, p. 212–242.

LOEBLICH, A. R., & TAPPAN, H., 1957, Correlation of the Gulf and Atlantic Coastal Plain Paleocene and Lower Eocene formations by means of planktonic Foraminifera: Jour. Paleontology, v. 31, p. 1109–37.

——, ——, BECKMANN, J. P., BOLLI, H. M., MONTANARIO GALLITELLI, E., & TROELSEN, J. C., 1957, Studies in Foraminifera: U. S. Natl. Mus., Bull 215, 323 p., 74 pls.

SCHMIDT, F., 1959, Biostratigraphie du Campanien-Maastrichtien du nordest de la Belgique sur la base des Bélemnites: Ann. Soc. geol. Belgique, v. 82, p. 235–56.

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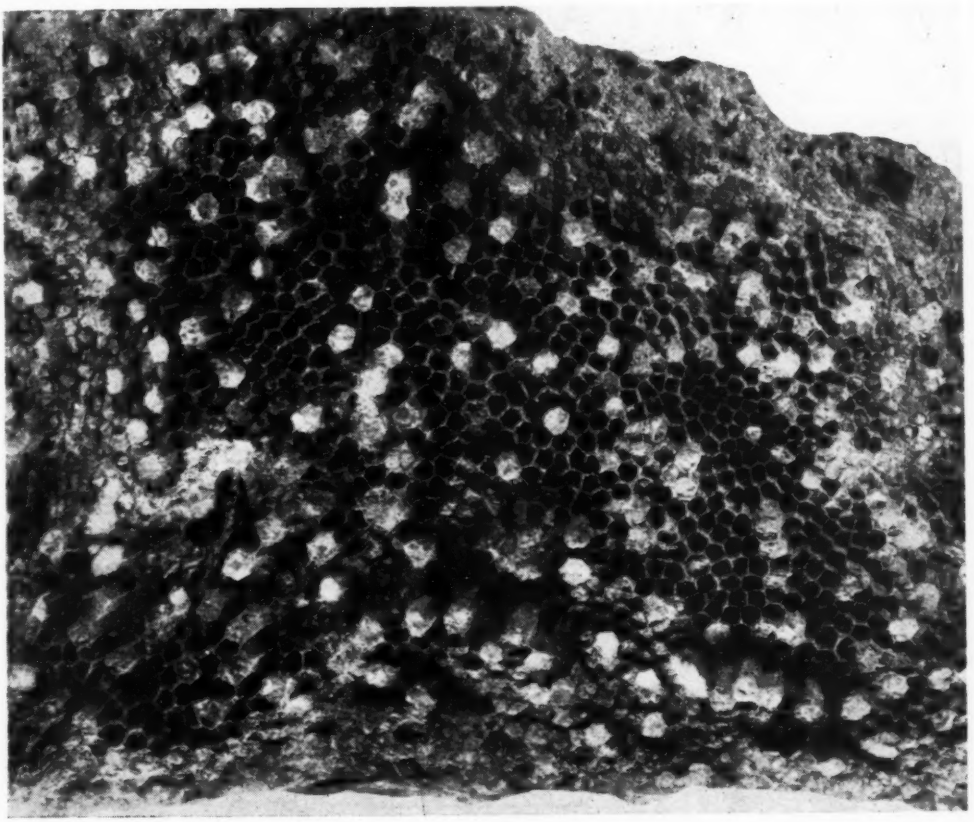
JOURNAL OF PALEONTOLOGY, V. 34, NO. 3, P. 589–601, 1 TEXT-FIG., MAY, 1960

PALEONTOLOGICAL NOTES

THE HOLOTYPE OF *FAVOSITES BILOCULI* HALL

ERWIN C. STUMM
Museum of Paleontology, University of Michigan



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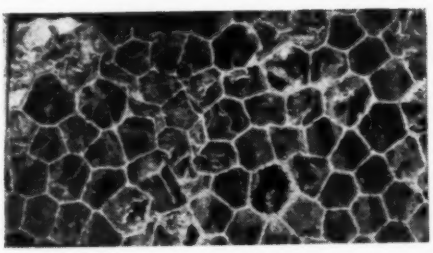

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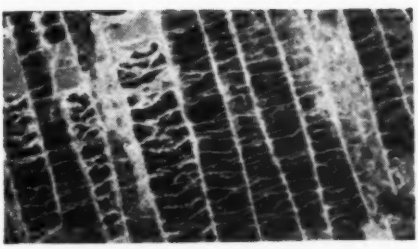


c

TEXT-FIG. 1—a, distal surface of holotype of *Favosites biloculi* Hall, ×1; b, transverse section of holotype, ×2; c, longitudinal section of holotype, ×2.

James Hall, in his "Illustrations of Devonian Fossils" (1876 or 1877, pl. 7, fig. 2) figured a specimen which he indicated on the plate explanation to be *Favosites epidermata?* var. *biloculi*. No subsequent reference has been made to this species except that Fenton and Fenton (1936, p. 36) mentioned that the type had not been traced and "that there was no ground, therefore, on which *biloculi* may be retained." The holotype was recently found by Mr. C. W. Kilfoyle, Curator of the Paleontological Collections at the New York State Museum. I am very grateful to Mr. Kilfoyle for the opportunity to study the specimen.

It is especially fortunate that the type has been found as the species is common in the Lower Onondaga limestone of New York and southwestern Ontario, the Bois Blanc formation of Michigan, on the coral bed of the Jeffersonville limestone of the "Falls of the Ohio." The species is a true *Favosites* and has no close relationship to *Emmonsia epidermata* (Rominger).

SYSTEMATIC DESCRIPTION

Genus FAVOSITES Lamarck

FAVOSITES BILOCULI Hall

Text-fig. 1

Favosites epidermata? var. *biloculi* Hall, 1876 or 1877, pl. 7, fig. 2.

Description.—Corallum large, low hemispherical to discoid, composed of pentagonal or hexagonal corallites. Majority of corallites averaging 2.5 mm. in diameter with occasional ones having diameters ranging from 3.0 to 3.5 mm. Calyxes with erect, smooth walls and flat bases formed by the uppermost tabulae. Mural pores biserial or triserial, in parallel rows. In transverse section corallite walls smooth, with no trace of squamulae, septal spines, or septal ridges. In longitudinal section tabulae typically complete, horizontal or slightly undulating, spaced from .5 to 1.5 mm. apart.

Remarks.—The internal structures have been partly altered by silicification but are still discernible. The specific name *biloculi* refers to the two sizes of corallites.

Occurrence.—Middle Devonian, lower part of Onondaga limestone, Caledonia, New York.

Type.—Holotype No. 11265, New York State Museum.

REFERENCES

HALL, JAMES, 1876 or 1877. Illustrations of Devonian Fossils: Corals of the Upper Helderberg and Hamilton groups. Weed Parsons and Company, Albany, New York.

FENTON, C. L., & FENTON, M. A., 1936. The "Tabulate" corals of Hall's "Illustrations of Devonian Fossils." Ann. Carnegie Mus., v. 25.

NEW FOSSIL BALANID LOCALITIES IN HUNGARY

G. KOLOSVÁRY

Syst.-zool. inst. of the University, Szeged, Hungary

Balanus concavus Bronn

1. Gyöngyöspata, Danka River in Tortonian (F. Legányi 1951).
2. Nekézseny, Mt. Bükk, Comitat Borsod, SE. in Aquitanian-Burdigalian G. Kolosváry 1950).
3. Dédes-Dezsö valley, Mt. Bükk in Helvetian (F. Legányi 1951).
4. Abod, Mt. Szendrö, in Burdigalian. (A. Jámbor 1958).

Balanus tintinnabulum Linné

1. Nekézseny, Mt. Bükk, Comitat Borsod, SE. in Aquitanian-Burdigalian.
2. Almár Valley, Mt. Bükk, Comitat Borsod, in Burdigalian (F. Legányi 1951).

Balanus laevis Darwin

1. Fót, Hungary N. in Aquitanian-Burdigalian (H. Vereb & G. Kolosváry).
2. Gyöngyöspata, Danka River in Tortonian (F. Legányi 1951).

Balanus amphitrite litoralis Kolosváry

1. Fenyönyárád, Comitat Borsod, in Burdigalian (L. Badócz 1958).

Balanus perforatus Bruguière

New addition to the fossil fauna of Hungary. Locality: Bekonygyepes near Devecser 300 m. in Mt. Bakony in Tortonian. Diameter of the orifice 11×9 mm. Diameter of the base 24×19 mm. Three specimens were found. They have been placed in the Geological Institution, Budapest, Hungary, 1955.

GEOGRAPHIC DISTRIBUTION OF *PLANORBULA VULCANATA* LEONARD IN NEBRASKA

LARRY FRANKEL
University of Connecticut

In his study of the Pleistocene mollusca fauna of the mid-continent region, A. B. Leonard has described many new pulmonate species. One of these, apparently restricted to Yarmouthian deposits, is *Planorbula vulcanata* which Leonard (1948) divides into two subspecies, *P. v. vulcanata* and *P. v. occidentalis*.

The distribution of the subspecies as reported by Leonard (1948, 1950), Frye, Swineford & Leonard (1948) and Frye & Leonard (1952) is as follows: (note: numbers following county name refer to locations on text figure 1).

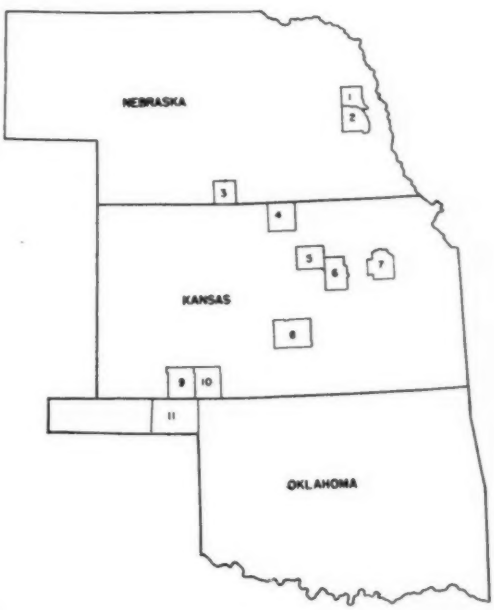
Planorbula vulcanata vulcanata:

Harlan (3) County, Nebraska; Jewett (4), Ottawa (5), Dickensen (6), Wabaunsee (7) and Clark (10) Counties, Kansas.

Planorbula vulcanata occidentalis:

Reno (8) Meade (9) and Clark (10) counties, Kansas; Beaver (11) County, Oklahoma.

This apparently restricted distribution of *Planorbula vulcanata occidentalis* led Leonard (1950, p. 18) to conclude that this was a southwestern race of the typical species.



TEXT-FIG. *1*—Map showing known distribution of *Planorbula vulcanata* by counties (for ceunty names see text.)

Subsequent to publication of Leonard's data new discoveries were made in eastern Nebraska. Wakely (1954) reported *Planorbula vulcanata* from Sappa (Yarmouth) alluvial sediments along the Pebble Creek tributary of the Elkhorn River, approximately one mile south and west of Scribner, Dodge County, Nebraska (NE¼ sec. 6 T19N, R6E). (See location 1, text figure 1.). These specimens (examined by the writer) have great variability; individuals can be assigned to both named subspecies and to intermediate groups.

The writer (Frankel, 1956) collected specimens of *Planorbula vulcanata* from alluvial sediment in the south bluff of the Platte River, about 2½ miles northeast of Cedar Bluffs, Saunders County, Nebraska (NE¼ sec. 23 T17N, R7E) (See loc. 2, text-fig. 1). From its stratigraphic position the sediment was tentatively identified as Sappa. Like Wakely's specimens these

forms are highly variable in character; most, however, are best ascribed to *P. v. occidentalis*.

In view of the above data the geographic range of the species must be extended to the northeast, and Leonard's hypothesis that *Planorbula vulcanata occidentalis* is a southwestern race of the typical species must be abandoned.

REFERENCES

FRANKEL, L., 1956, Pleistocene geology and paleoecology of parts of Nebraska and adjacent areas: Univ. Nebraska, Dept. Geology, unpublished Ph.D. dissertation, 297 p.

FRYE, J. C., Swineford, A., & LEONARD, A. B., 1948, Correlation of Pleistocene deposits of the Central Great Plains with the glacial Section: Jour. Geology, v. 56, no. 6, p. 501–525.

——, & LEONARD, A. B., 1952, Pleistocene Geology of Kansas: Kans. Geol. Survey, Bull. 99, 230 p.

LEONARD, A. B., 1948, Five new Yarmouthian planorbid snails: Nautilus, v. 62, p. 41–47.

——, 1950, A Yarmouthian molluscan fauna in the mid-continent region of the United States: Univ. Kansas Pal. Contr., Mollusca, art. 3, 48 p.

WAKELY, WM., 1954, Fossil gastropods from the Pleistocene terrace-fills of the Elkhorn River Valley, Nebraska: Univ. Nebraska, Department of Geology, unpublished M.S. thesis, 70 p.

NOTE ON SOME SPECIES OF OSTRACODA DESCRIBED BY A. M. NORMAN

W. A. VAN DEN BOLD
Louisiana State University

Some of the Rev. A. M. Norman's descriptions of new species of Ostracoda appear to have been overlooked by most later workers. This is not surprising in view of the fact that some of these descriptions occur in reports by others, so that they are difficult to locate, the more so, since Norman often does not refer to them in his later publications.

One of these descriptions is found in a "Report on the Dredging of the Northumberland Coast and Dogger Bank, drawn up by Henry T. Mennell, on behalf of the Natural History Society of Northumberland, Durham and Newcastle-on-Tyne, and of the Tyneside Naturalists' Fieldclub," which appeared in the "Report of the Thirty-second Meeting of the British Association for the Advancement of Science; held in Cambridge in October 1862," published in 1863 (Mennell, 1863). This report contains the description of one new ostracod species, *Cythere limicola* Norman (p. 119). Later authors (e.g. Hirschmann, 1916, p. 580; Elofson, 1941, p. 277; Triebel, 1949, p. 188, 189 and Howe, 1955, p. 580) have indicated the type species of *Palmenella* as "*Cythereis limicola* Norman, 1865 (p. 20, pl. 6, figs. 1–4)." However, the "Natural History Transactions of Northumberland and Durham, being papers read at the Meetings of the Natural History Society of Northumberland, Durham and Newcastle-on-Tyne and the Tyneside Naturalists' Fieldclub, 1865–67, vol. 1," to which they refer, was not published until 1867.

Further confusing is the fact that Norman in his 1867 paper indicates several species as n. sp., while in reality they had been described earlier by himself, in the case of *Cythereis limicola* even twice. The other publication in which they occur as n. sp. of Norman is: Brady, 1865, "Deep-Sea Dredging on the Coasts of Northumberland and Durham in 1864," published in the "Report of the Thirty-fourth Meeting of the British Association for the Advancement of Science; held in Bath in September 1864" (p. 189–193), which appeared in 1865.

In his synonymies, Norman (1867) quotes some of his species in Brady 1865 as M.S., thus throwing doubt on the real date of publication of the quoted paper. In some cases (*Cythere guttata* and *Cythere multifora*) he even refers to them under different names suggesting that he had time to change these names before the paper (Brady 1865) was printed. In the same publication (Norman 1867) he also quotes in the synonymy of *Cythere latissima* n. sp., a "Cythere obesa

Norman, M.S., Trans. Tyneside Natural. Fieldclub, vol. 5, p. 266, but not *C. obesa* of Reuss," which paper was published in 1863. Moreover he does not quote any synonymy for *Cythereis limicola* n. sp., although we have seen that the first description of this species was also in 1863 and a comparison of this earlier description with his later figures shows that it is very probably the same species.

It appears, therefore, that Norman considered these earlier descriptions without figures as preliminary and without nomenclatorial value and that this is the reason why he refers to them as M.S. or not at all. However, where complete descriptions were given, these earlier ones should be regarded as describing the species for the first time and the species should carry the date of the earlier publication.

Species occurring in these publications and often not quoted correctly by later workers, including Norman, are:

LOXOCONCHA GUTTATA (Norman)

1) *Cythere guttata* Norman n. sp., Brady 1865, p. 192.
2) *Cythere guttata* Norman n. sp., Norman 1867, p. 19, pl. VI, figs. 9–12. (Refers to 1 as *Cythere concentrica* Norman M.S., but not of Reuss or Williamson).

LOXOCONCHA MULTIFORA (Norman)

1) *Cythere multifora* Norman n.sp., Brady 1865, p. 192.
2) *Cythere multifora* Norman n.sp., Norman 1867, p. 18, pl. VI, figs. 13–16. (Refers to 1 as *Cythere rugosa* Norman M.S., but not *C. rugosa* of Speyer).

HIRSCHMANNIA LAEVATA (Norman) = H. TAMARINDA (Jones)?

1) *Cythere laevata* Norman n.sp., Brady 1865, p. 192.
2) *Cythere laevata* Norman n.sp., Norman 1867, p. 18, pl. V, figs. 13–16 (no reference to 1).

EUCYTHERE DECLIVIS (Norman)

1) *Cythere declivis* Norman n.sp., Brady 1865, p. 192.
2) *Cythere declivis* Norman n.sp., Norman 1867, p. 16, pl. V, figs. 9–12 (no reference to 1).

EUCYTHERIDEA BRADII (Norman)

1) *Cythere* n.sp., Norman 1863, p. 266.
2) *Cythere Bradii* Norman n.sp., Brady 1865, p. 192,193 (no reference to 1).
3) *Cythere debilis* (Jones), Norman 1867, p. 15, pl. V, figs. 5–8 (refers to 2 as M. S.).
4) *Cythere Bradii* Norman, Norman 1867, p. 29 (refers to 1).

TRACHYLEBERIS DUNELMENSIS (Norman)

1) *Cythereis dunelmensis* Norman n.sp., Brady 1865, p. 193.
2) *Cythereis dunelmensis* Norman n.sp., Norman 1867, p. 22, pl. VII, figs. 1–4 (no reference to 1).

PALMENELLA LIMICOLA (Norman)

1) *Cythere limicola* Norman n.sp., Norman 1863, p. 266 (nom. nud.).
2) *Cythere limicola* Norman n.sp., Mennell 1863, p. 199 (no reference to 1).
3) *Cythereis limicola* Norman n.sp., Brady 1865, p. 193 (no reference to 1 or 2).
4) *Cythereis limicola* Norman n.sp., Norman 1867, p. 20, pl. VI, figs. 1–4 (no reference to 1,2 or 3).

CYTHEROPTERON LATISSIMUM (Norman)

1) *Cythere obesa* Norman n.sp., Norman 1863, p. 266 (nom. nud.).
2) *Cythere latissima* Norman n.sp., Brady 1865, p. 191,192 (no reference to 1).
3) *Cythere latissima* Norman n.sp., Norman 1867, p. 19, pl. VI, figs. 5–8 (refers to 1 and 2, adds "but not *C. obesa* of Reuss."

Since Reuss described *Cytherina obesa* (1850, p. 56, pl. 8, figs. 26a,b) as compared to *Cythere obesa* of Norman, this does not constitute a case of objective synonymy. The fact that Norman did not describe *Cythere obesa* saves us from a complication in the nomenclature of this species.

JONESIA SIMPLEX (Norman)

1) *Cythere acuta* Baird, Norman 1863, p. 266.
2) *Cythere acuta* Norman, Mennell 1863, p. 199.
3) *Cythere simplex* Norman n.sp., Norman 1867, p. 17, pl. V, figs. 1–4, not *C. acuta* Baird.

HEMICYTHERURA CELLULOSA (Norman)

Cythere cellulosa Norman n.sp., Norman 1867, p. 22, pl. V, figs. 17–20, pl. VI, fig. 17.

BIBLIOGRAPHY

BRADY, G. S., 1865, Deep-Sea Dredging on the Coasts of Northumberland and Durham in 1864. Brit. Assoc. Adv. Sci., Rep. of 34th Meeting, Sept. 1864, p. 189–193F, London, 1865.

ELOFSON, O., 1941, Zur Kenntnis der marinen Ostracoden Schwedens mit besonderer Berücksichtigung des Skageraks. Zool. Bidr. Uppsala, Bd. 19, 543 p.

HIRSCHMANN, N., 1916, Ostracoda of the Baltic sea, collected by N. M. Knipovitch and S. A. Pavlovitch in the summer of 1908. Ann. Mus. Zool. Imp. Acad. Sci., v. 20, pl 569–597, Petrograd, 1915.

HOWE, H. V., 1955, Handbook of Ostracod Taxonomy. Louisiana University Studies, Physical Science ser. No. 1, 389 p.

MENNELL, H. T., 1863, Report on the Dredging of the Northumberland coast and Dogger Bank, drawn up by Henry T. Mennell, on behalf of the Natural History Society of Northumberland, Durham and Newcastle-on-Tyne and of the Tyneside Naturalists' Field-club. Brit. Assoc. Adv. Sci., Rep. 32nd Meeting, Oct. 1862, p. 118–122, London, 1863.

NORMAN, A. M., 1863, Report on the Crustacea, in Mennell, H. T.: Report of the Dredging Expedition to the Dogger Bank and the Coasts of Northumberland. Trans. Tyneside Naturalists' Fieldclub, V, Newcastle-on-Tyne, 1862, p. 263–267, Ostracoda p. 266.

——, 1867, Report on the Crustacea, in Brady, G. S.: Reports of Deep Sea Dredging on the Coasts of Northumberland and Durham, 1862–1864. Nat. Hist. Trans. Northumberland and Durham 1, p. 12–29, pl. 5–7, London 1867.

REUSS, A. E., 1850, Die fossilen Entomostraceen des österreichischen Tertiärbeckens. Haidingers Naturwiss. Abh., Bd. III, Abt. 1, 1849, p. 6–92, pls. 8–11.

TRIEBEL, E., 1949, Mikropaläontologische Kennzeichnung der Ostracoden-Gattungen *Xenocythere* und *Palmenella*. Senckenbergiana, Bd. 30, p. 185–192, pls. 1,2, Frankfurt a. Main, 1949.

AN EMENDATION OF THE DESCRIPTION OF *NODOSARIA CATESBYI*, D'ORBIGNY

JOSEPH WILLIAM SABOL
McLean Paleontological Laboratory, Alexandria, Virginia

During a study of an unconsolidated sample of Yorktown (upper Miocene) from Surry County, Virginia, the writer noticed a particular fact concerning *Nodosaria catesbyi*, d'Orbigny. This species, as reported by Cushman and Cahill (1933), may be identified as being composed of two chambers; the proloculum, which is subglobular with a short basal spine, and a second chamber more pyriform, apertural end somewhat prolonged. This description corresponds with the original description by d'Orbigny (1839).

In the study of the Yorktown material the writer noted specimens of *Nodosaria catesbyi* that were made up of more than two chambers. One specimen had three distinctly differentiated chambers while others had four. Other characteristics of the specimens complied with the description as given by Cushman (1930), Cushman and Cahill (1933), and d'Orbigny (1839). The recognitions of the additional chambers does not, in the author's opinion, necessitate the erection of a new species or sub-species; rather it is felt that it is an expression of variation in form within the original species.

This same situation was noted by McLean (1956, p. 329) in a sample of the Yorktown from Carter's Grove, Virginia. It is interesting to note that the sample studied by the author is considered to be stratigraphically similar to the Carter's Grove sample of McLean. McLean reported no other specimen of *Nodosaria catesbyi* from any other locality of Yorktown material that he studied, and its occurrence at the Carter's Grove outcrop was noted as being rare.

BIBLIOGRAPHY

D'ORBIGNY, ALCIDE, 1839, *in* De la Sagra, Histoire physique, politique et naturella de l' ile de Cuba Foraminiferes, p. 16, pl. 11, figs. 8–10.

CUSHMAN, J. A., 1930, The Foraminifera of the Choctawhatchee Formation of Florida, Fla. Geol. Sur. Bull. 4, p. 28, pl. 5, fig. 4.

——, & CAHILL, E. D., 1933, Miocene Foraminifera of the Coastal Plain of the Eastern United States, U.S.G.S. Prof. Paper 175-A, p. 14, pl. 5, fig. 5.

MCLEAN, J. D. JR., 1956, The Foraminifera of the Yorktown Formation in the York-James Peninsula of Virginia, with notes on the Associated Mollusks, Bull. Am. Paleontology, v. 36, no. 160, p. 329, pl. 39, figs. 1–4.

METHODS OF MEASURING THE INTERNAL VOLUME OF SHELLS

LOUIS S. KORNICKER
Institute of Marine Science, The University of Texas

The internal volume of a pelecypod valve may be measured by: (A) dipping the valve into a container of water and then pouring the water in the shell into a graduated cylinder; (B) filling the inverted valve with water measured from a burette; or by a method (C) described in this note.

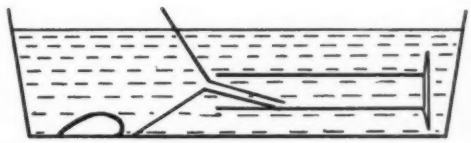
In method C the valve is placed concave downward on the bottom of a vessel which is then filled with water. The shell is held on the bottom with one hand. A funnel and graduated cylinder are placed in the vessel and allowed to fill with water (text-fig. 1). The stem of the funnel is placed inside the graduated cylinder and the funnel with cylinder is inverted over the shell (text-fig. 2). The shell is held concave downward on the bottom with the fingers of one hand during step 2. The shell is then inverted permitting the entrapped air under the shell to escape and displace water in the graduated cylinder. The volume of air may be read directly from the scale on the graduated cylinder (text-fig. 3).

The three methods were compared on shells of the pelecypod *Dinocardium robustum*. Internal volume measurements made using methods A and C were about the same (Table 1). Methods A and C resulted in higher volume measurements than

TABLE 1—COMPARISON OF INTERNAL VOLUME MEASUREMENTS OF *Dinocardium robustum* VALUES OBTAINED BY DIFFERENT MEASURING TECHNIQUES

Specimen Number	Type Valve	Internal Volume Measurements		
		Method A (Avg. of 5 trials, cc.)	Method B (Avg. of 2 trials, cc.)	Method C (Avg. of 5 trials, cc.)
2	Right	49.0	—	50.0
4	Right	49.1	—	47.2
4	Left	47.2	40.8	45.6
5	Left	50.6	45.0	—
6	Right	105.0	—	102.0
6	Left	—	79.7	82.0
7	Right	8.0	—	7.5
10	Left	119.0	108.2	118.0

1.



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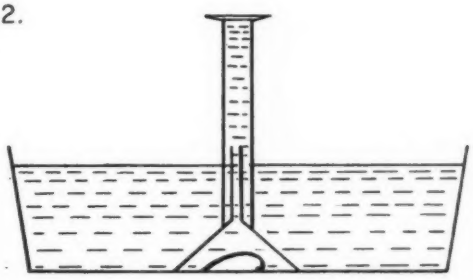

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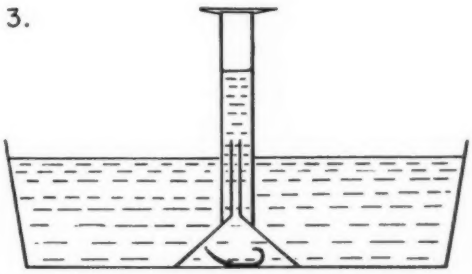


TEXT-FIG. *1*—The shell is placed on bottom of vessel which is then filled with water. A funnel and graduated cylinder are placed in the vessel and allowed to fill with water. The shell is held in place with one hand (not shown).

TEXT-FIG. *2*—The funnel stem is placed inside a graduated cylinder and both are inverted over the shell. The shell is held in place with the fingers of one hand (not shown).

TEXT-FIG. *3*—The shell is overturned under the funnel. The air that escapes from under the shell displaces water in the graduated cylinder. The volume of displaced water is read directly from the scale of the graduated cylinder.

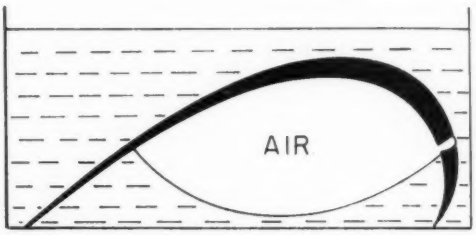
did method B (Table 1). It has not been determined which method better approximates the true volume. Method A has the advantage of simplicity and rapidity. Method B probably gives least reproduci-

TABLE 2—COMPARISON OF THE COEFFICIENT OF RELATIVE VARIATION OF INTERNAL VOLUME MEASUREMENTS OF *Dinocardium Robustum* VALVES MADE WITH METHODS A AND C

Method of Measuring	Specimen Number	Type Valve	Number of Measurements	Observed Range (cc.)	Arithmetic Average (cc.)	Standard Deviation (cc.)	Coefficient of Relative Variation
C	4	Right	5	45.2–48.5	47.2	1.16	2.45%
A	4	Right	5	47.6–50.0	49.1	0.99	2.00%
C	4	Left	5	42.0–49.5	45.6	2.69	5.90%
A	4	Left	5	45.5–49.0	47.2	1.29	2.73%

bility by different operators because judgement is involved in deciding when the shell is to be considered filled with water. Method C has almost the same degree of reproducibility as method A (Table 2). The accuracy of method C may be increased by adjusting the water level in the large vessel so that it is the same as the water level in the graduated cylinder when readings are made.

Method C was devised specifically to determine the volume of air entrapped beneath pelecypod valves containing holes drilled by snails when the valves are in a concave downward position and covered with water (text-fig. 4). The amount of air entrapped beneath the valves depends on the diameter and position of the snail-drilled-hole so that it is not possible to make this measurement using either method A or B.



TEXT-FIG. 4—Cross-section of pelecypod shell with snail-drilled-hole showing entrapped air.

OCCURRENCE OF FORAMINIFERA AND CONODONTS IN UPPER PALEOZOIC AND TRIASSIC ROCKS, NORTHERN ALASKA[1]

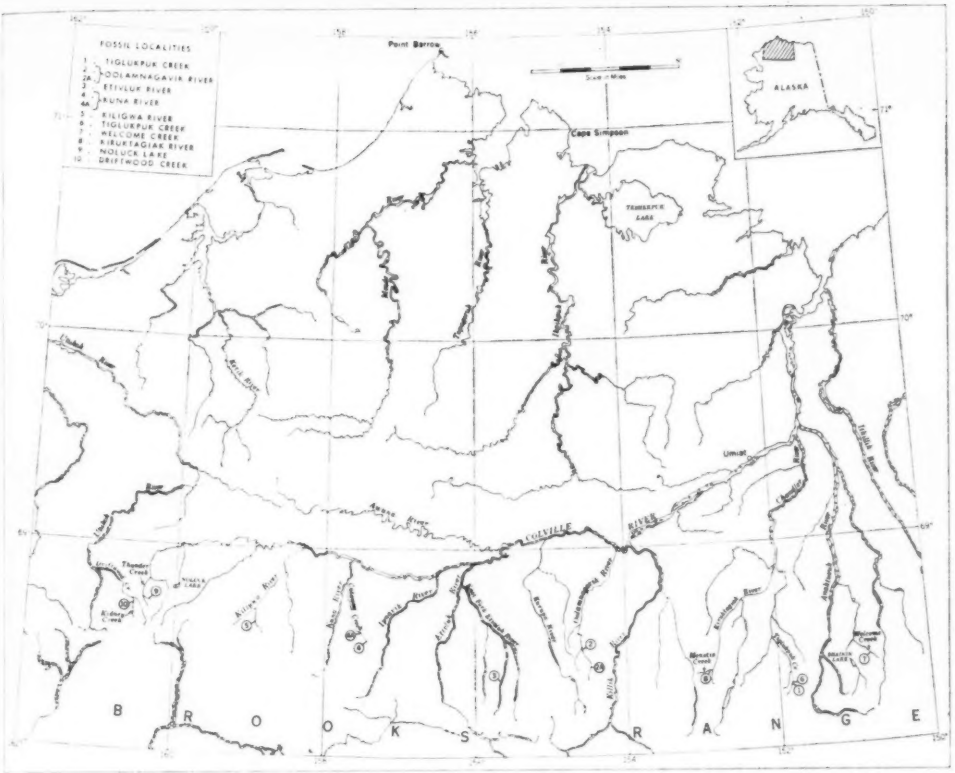
HARLAN R. BERGQUIST
U. S. Geological Survey

INTRODUCTION

Agglutinate Foraminifera of late Paleozoic age and fragmented compound and plate-like conodonts that are apparently of Middle to Late Triassic age have been found in rock samples collected from the Siksikpuk formation (Permian?) and Shublik formation (Triassic) in northern Alaska. These known occurrences are at widely separated localities (text-fig. 1) between long 150°43'W and 160°30'W, in a narrow belt of outcropping Paleozoic and Triassic rocks which parallels the north front of the Brooks Range. The samples were collected for general microfossil studies by U. S. Geological Survey geologists during the 1949, 1950, and 1951 field seasons. Some of the sample material, as well as slides prepared in the Survey laboratory at Fairbanks, Alaska, was examined by Wilbert H. Hass in 1951 and 1957. Hass identified the genus *Gondolella* in a few of the samples and recognized a fragment of *Hindeodella* in one sample (written communication).

No further work has been done in this belt of Paleozoic and Triassic rocks since 1951, and relatively few samples of Triassic

[1] Publication authorized by the Director, U. S. Geological Survey.



TEXT-FIG. 1—Index map of northern Alaska showing location of fossil collections.

rocks were collected. Thus it has not been possible to secure additional material to fully evaluate the occurrences of the conodonts or to enlarge the collection of Paleozoic Foraminifera. In view of the recent papers describing conodonts in rocks of Early Triassic age in Idaho, Nevada, and Utah by Youngquist (1952), Müller (1956), and Clark (1959), however, reappraisal of the conodont occurrences in Alaska is needed. Furthermore, the intensified search for petroleum in Alaska in the last two or three years has stimulated interest in all phases of Alaskan stratigraphy and paleontology. Thus this note is intended only to document the few presently known occurrences in Alaska of late Paleozoic Foraminifera in the Siksikpuk formation and of conodonts in rocks that are now recognized as of Middle to Late Triassic age, as heretofore this information has not been published.

Most of the conodonts and Paleozoic Foraminifera in the Alaskan collection came from samples from the Tiglukpuk Creek area (text-fig. 1) where the Shublik formation disconformably overlies the Siksikpuk formation. Other collections came from widely separated localities where only one or the other of the formations is exposed; they are briefly discussed here to indicate the geographic distribution of these fossils.

FORAMINIFERA OF THE SIKSIKPUK FORMATION

Tiglukpuk Creek area, collection 1: The largest collection of late Paleozoic Foraminifera is from the Tiglukpuk Creek area. William W. Patton, Jr., and A. S. Keller collected a few samples from a section of approximately 300 feet of red and green shale and siltstone exposed in a cutbank on the east side of a small tributary to Tiglukpuk Creek at about lat 68°17′N and long

151°48′W. These beds crop out above strata of Mississippian age and below the Triassic Shublik formation. The section was designated the type locality of the Siksikpuk formation by Patton (1957, p. 41) and described as follows:

> "The Siksikpuk formation is composed chiefly of variegated green, gray, and dark red shale and siltstone that locally are notably calcareous, cherty, or ferruginous. All gradations from thin, fissile clay shale to platy silty shale to 6-inch beds of siltstone occur. Ellipsoidal concretions of barite characterize the lower two-thirds of the sequence. The variegated nature and the bright yellow and orange weathering of the ferruginous beds serve to distinguish, even at a distance, the Siksikpuk formation from the gray limestone and dark shale and chert of the underlying Lisburne group and from the dark shale of the overlying Shublik formation."

A Permian age was suggested from identifications of corals by Helen Duncan and of brachiopods by J. Thomas Dutro, Jr. (Patton, 1957).

Foraminifera in the red and green shale samples of the type section of the Siksikpuk formation include the following: tubular sections and initial bulbous portions of one or more species of *Hyperammina;* compressed tests of a species of *Thurammina;* segments of a robust form of *Reophax?;* common to abundant large and small tests of a species of *Involutina;* small specimens of *Glomospira* sp. and a few large contorted specimens similar to *Glomospira articulosa* Cushman and Waters; small flattened tests of *Glomospirella* sp. in one sample and a few tests of a slender delicate form of *Ammobaculites* in 2 samples; and robust tests of a biserial form which is more or less the same width throughout and is quadrate in apertural end view. The last mentioned may belong either to *Spiroplectammina* or possibly to *Mooreinella,* as the initially coiled portion is not clearly discernible and appears to be more trochoid than planispiral. In addition there are two or more species of *Trochammina.* Some specimens resemble *T. arenosa* Cushman and Waters of the Middle and Upper Pennsylvanian of Texas, and some are similar to *T. grahamensis* Cushman and Waters of the Upper Pennsylvanian of Texas (Cushman and Waters, 1930, p. 68–69). Specimens are for the most part stained red or have a greenish cast, depending on the rock type from which they came.

Oolamnagavik River area, collections 2 and 2a: A foraminiferal fauna consisting of abundant specimens of a large species of *Involutina,* a few tubular and compressed sections of *Hyperammina* sp., compressed specimens of *Thurammina* sp. and a few tests of *Spiroplectammina?* or *Mooreinella?,* plus a few discoidal Radiolaria (Cenodiscidae?) was found in two samples collected in 1950 by R. M. Chapman from beds of the Siksikpuk formation along the west fork of the Oolamnagavik River at lat 68°32′N., long 154°31′W. and lat 68°28′N., long 154°27′W. This is approximately 65 miles west of the type locality of the Siksikpuk formation in the Tiglukpuk Creek area.

Etivluk River area, collection 3: In 1950, C. D. Reynolds collected samples from the Siksikpuk formation along the east fork of the Etivluk River (lat 68°22′N., long 155°35′W.) which yielded numerous red-stained specimens of the same large species of *Involutina,* plus fragments of a few other agglutinate Foraminifera.

Kuna River area, collections 4 and 4a: Foraminifera of the Siksikpuk formation were also found in two samples from red and green shale collected by I. L. Tailleur near the headwaters of Cutaway Creek, tributary to Kuna River, at lat 68°33′N., long 157°28′W. and lat 68°35′N., long 157°33′W., approximately 140 miles west of the type locality of the Siksikpuk formation. In one sample there were numerous sections of *Hyperammina* sp. and specimens of *Involutina* sp., plus a few specimens of *Thurammina* sp., *Glomospira* sp. and *Trochammina* sp. aff. *T. arenosa* Cushman and Waters. The other sample yielded abundant specimens of *Involutina* sp., fragments of *Hyperammina* sp., a few specimens of *Glomospira* sp., *Ammobaculites* sp. (narrow form), and *Trochammina* sp.

Conodonts associated with Foraminifera, Siksikpuk formation (?)

Kiligwa River area, collection 5: Broken conodonts and agglutinated Foraminifera similar to species from the Siksikpuk forma-

tion in the Tiglukpuk Creek area were found in a sample of presumed Permian age collected by B. H. Kent from the Kiligwa River area, approximately 180 miles west of the type locality of the Siksikpuk formation. All the microfossils in this sample are stained red. The conodonts are a large species of *Gondolella* and have smooth platforms and low nodes along the axis. Specimens appear to be much like species described from the Permian Phosphoria formation of Idaho (Youngquist, 1951). To date this occurrence of conodonts in late Paleozoic rocks is the only one known in the Alaskan collections.

Conodonts and associated Foraminifera, Shublik formation

Tiglukpuk Creek area, collection 6: In 1950, samples were collected by Patton from black shale of the Shublik formation of Triassic age which overlies the Siksikpuk formation. Concerning these beds, Patton and Matzko (1959, p. 7) state:

> The Shublik formation is composed principally of highly carbonaceous grayish-black shale, chert, and limestone. The dark color distinguishes it from the variegated rocks of the underlying Siksikpuk formation. In the Tiglukpuk Creek and upper Kiruktagiak River areas the Shublik formation can be subdivided into three members: (a) the lower member of black, gray, and greenish-gray shale with minor intercalated dark limestone; (b) a middle member of dark siliceous limestone, black paper shale, and dark, calcareous shale; and (c) an upper member of dark, fossiliferous limestone capped by dark shale.

The lower member of the Shublik formation in this area is more than 500 feet thick and has an ammonite-pelecypod fauna which has been dated as early Middle Triassic by Bernhard Kummel (Patton and Matzko, 1959, p. 8). The middle and upper members of the Shublik formation as delimited by Patton in the same area are approximately 150 feet and 80 feet thick, respectively, and have a typical Late Triassic assemblage of fossils including *Monotis subcircularis* (Gabb) and *Halobia* sp. (Patton and Matzko, 1959, p. 8).

Seven samples for microfossil studies were collected from the lower member of the Shublik formation and one sample from each of the other two members. A small foraminiferal fauna was found in these samples, with fragments of compound and plate-like conodonts in every sample above the lowest 100 feet.

Only very rare to rare fragments or broken specimens of compound conodonts were in the material from the middle part of the lower member; the samples from the uppermost 150 feet of the member contained common to abundant plate-like conodonts as well as numerous fragments of the compound type. Several specimens of plate-like conodonts and very abundant fragments of compound forms were found in the sample from the middle member of the Shublik formation, but only two fragments of compound conodonts were in the sample from the upper member.

Foraminifera in the samples from the lower member of the Shublik formation include segments of *Tolypammina*, a small species of *Involutina*, a small form of *Gaudryina*, delicate tests of a small *Ammobaculites*, a slender species of *Spiroplectammina*, and, in the uppermost 100 feet of the member, a few specimens of *Rectoglandulina lata* (Tappan) and *R. simpsonensis* (Tappan).

The middle and upper members of the Shublik formation yielded only a few specimens of *Astacolus connudatus* Tappan, *Nodosaria shublikensis* Tappan, and *Rectoglandulina simpsonensis* (Tappan). These three species and *R. lata* (Tappan) (found in the lower member) were described by Mrs. Loeblich (Tappan, 1951) from beds of the Shublik formation of Late Triassic age in the Sadlerochit River area, northeastern Alaska (east of the area of text-fig. 1), and from equivalent subsurface beds in wells in the Point Barrow and Cape Simpson areas.

Welcome Creek area, collection 7: Conodonts were found in two of six microfossil samples collected by Patton in 1950 from beds of the Shublik formation in the Welcome Creek area, approximately 25 miles northeast of the Tiglukpuk Creek area (approximately lat 68°25′N., long 150°48′W.), or about 6 miles northeast of Shainin Lake. One sample contained numerous broken specimens of plate-like conodonts (gondolellids) along with a few fragments of compound conodonts, abundant specimens of

Astacolus connudatus, and a few specimens of *Nodosaria shublikensis*, *Rectoglandulina simpsonensis*, and *Vaginulinopsis acrula* Tappan. The Foraminifera suggest a Late Triassic age for the sample.

Although too fragmented for positive identification, some of the compound conodonts from the Tiglukpuk Creek and Welcome Creek areas can be tentatively identified as being hindeodellids and others as being prioniodinids. In addition there are two and possibly three species of *Gondolella* in these collections. The nodes along the axes of these specimens are generally larger and more denticulate than those present along the axis of the Permian(?) gondolellids from the Kiligwa River area.

Kiruktagiak River area, collection 8: A few fragments of compound conodonts were found in two samples collected in 1949 by I. L. Tailleur from beds of the Shublik formation exposed along Monotis Creek, a tributary of the Kiruktagiak River (see text-fig. 1). Two other samples collected by Patton in 1951 from the Shublik carried a few broken gondolellid conodonts. No other fossils were found in any of these samples which came from an area approximately 30 miles west of Tiglukpuk Creek at approximately lat 68°23′N., long 152°47′W. Lithologically the formation is similar in both areas, but here is much thinner, particularly the lower member which is only 100 feet thick (Patton and Matzko, 1959, p. 8). The samples probably are from the middle member.

Noluck Lake area, collection 9: A few conodonts were found in three samples of black shale collected by J. T. Dutro, Jr., from an outcrop north of Thunder Mountain along Thunder Creek, about 7 miles southwest of Noluck Lake (approximate lat 68°45′10″N., long 160°17′20″W.) (see text-fig. 1). Two samples were relatively high in the formation, above an occurrence of *Daonella?* sp. and about 60 to 75 feet below an occurrence of the Triassic pelecypod *Monotis subcircularis* (Gabb). The third sample came from a horizon about 100 feet below the *Monotis* bed. A few broken gondolellid specimens and numerous fragments of compound conodonts were found in the two higher samples along with silicified internal molds of chambers of nodosarian Foraminifera, a few specimens of *Lagena?* sp. and discoidal specimens of Radiolaria belonging to either the Cenodiscidae or the Phacodiscidae. The lower sample contained only fragments of compound conodonts and a few discoidal Radiolaria. A specimen of *Nodosaria shublikensis* in one of the higher samples suggests Late Triassic age.

Fragments of conodonts were common in a sample (collection 10) collected by E. G. Sable in 1950 from a rubble of shale and chert associated with *Monotis*-bearing limestone of the Shublik formation(?) in a cutbank on the east side of Kidney Creek, a tributary of Driftwood Creek, lat 63°43′10″ N., long 160°31′50″W. Hass identified *Gondolella* fragments, a *Hindeodella* fragment, and other fragments of blade-like, bar-like, and plate-like conodonts in material he examined from this sample (written communication).

CONCLUSIONS

Presence of conodonts in samples collected over a distance of more than 250 miles indicates their apparent distribution throughout the Triassic rocks of the northern foothills of the Brooks Range. Some of the occurrences are in rocks containing megafossils by which an age range from Middle to Late Triassic can be established. All the samples are from complexly faulted rocks of an overthrust zone, which might suggest that the conodont-bearing samples are not *in situ*. This is considered unlikely, however. Reworking of the fossils from Paleozoic strata is also considered unlikely, as the conodonts do not look worn. Furthermore, no conodonts were found in the type section of the Siksikpuk formation, which is overlain by the conodont-bearing Shublik formation. The presence of the conodonts in these Triassic rocks thus makes their time range greater than has been found elsewhere on the North American continent.

REFERENCES

CLARK, D. L., 1959, Conodonts from the Triassic of Nevada and Utah: Jour. Paleontology, v. 33, p. 305–312, pls. 44,45.

CUSHMAN, J. A., & WATERS, J. A., 1930, The Foraminifera of the Cisco Group of Texas: Univ. of Texas Bull. 3019, p. 23–81, pls. 1–12.

MÜLLER, K. J., 1956, Triassic conodonts from Nevada: Jour. Paleontology, v. 30, p. 818–830, pls. 95,96.
PATTON, W. W., JR., 1957, A new Upper Paleozoic formation, central Brooks Range, Alaska: U. S. Geol. Survey Prof. Paper 303-B, p. 41–43.
——, & MATZKO, J. J., 1959, Phosphate deposits in northern Alaska; U. S. Geol. Survey Prof. Paper 302–A, 17 p.
TAPPAN, HELEN, 1951, Foraminifera from the Arctic Slope of Alaska, part I, Triassic Foraminifera: U. S. Geol. Survey Prof. Paper 236-A, p. 1–20, pls. 1–5.
YOUNGQUIST, W. L., 1951, Phosphoria conodonts from southeastern Idaho: Jour. Paleontology, v. 25, p. 356–364, pl. 54.
——, 1952, Triassic conodonts from southeastern Idaho: *ibid.*, v. 26, p. 650–655.

NOMENCLATURAL NOTE

CORRECTION OF BRACHIOPOD NAMES

G. ARTHUR COOPER
U. S. National Museum

Dr. A. J. Rowell, University of Nottingham, England, who is preparing the section on Brachiopods for the Treatise on Invertebrate Paleontology, called my attention to two linguloids described in "*Chazyan and Related Brachiopods*," that are preoccupied:

Glyptoglossa Cooper, 1956, p. 226, is preoccupied by *Glyptoglossa* Brenske, 1895 (Ann. Mus. Stor. nat. Genova, vol. 35, p. 223—Coleoptera). For the preoccupied name I substitute *Glyptoglossella*, with type species *Glyptoglossa cavellosa* Cooper, 1957, p. 227.

Pachyglossa Cooper, 1956, p. 223, is preoccupied by *Pachyglossa* Hodgson, 1843 (Jour. Asiatic Sol. Bengal, vol. 12, p. 1009—Aves) and *Pachyglossa* Fauvel, 1868 (nom. nov. pro *Euryglossa* Fauvel, 1866, Bull. Soc. Linn. Normandie, (2), vol. 2, 1867, p. 379—Coleoptera). *Pachyglossella* is substituted with type species *Pachyglossa dorsiconvexa* Cooper, 1956, p. 225.

REFERENCE

COOPER, G. A. Chazyan and related brachiopods. Smithsonian Misc. Colls. v. 127, pts. 1 and 2, p. i–xvi, 1–1024, pls. 1–269.

JOURNAL OF PALEONTOLOGY, V. 34, NO. 3, P. 602–604, MAY, 1960

REVIEWS

CENOZOIC ECHINOIDS OF EASTERN UNITED STATES. C. Wythe Cooke. Geological Survey Professional Paper 321, 106 pp., 43 pls. For sale by the Superintendent of Documents, U. S. Government Printing Office, Washington 25, D. C. $3.00.

Fossil echinoids can be very useful to the stratigraphic paleontologist. Their stratigraphic range is usually short, their geographic distribution often wide, and identification relatively easy. Because of their scarcity, they are of little stratigraphic significance in Paleozoic rocks. However, in the Mesozoic and especially Cenozoic formations, they are often common and are valuable "markers." C. Wythe Cooke's paper will be of considerable assistance to stratigraphers working in the Cenozoic deposits of eastern United States.

One-hundred and forty-four species and subspecies, assigned to sixty genera and four subgenera, are described from the Atlantic and Gulf Coastal Plain of the United States and adjacent waters. Three new genera and eight new species are described. There is a detailed discussion of the stratigraphy and the faunas. The major usefulness of these echinoids for stratigraphic purposes is that almost all the species are restricted to a single time unit. For example, all the eighteen species known from the Paleocene are restricted to the Paleocene.

Dr. Cooke is to be commended especially for providing an excellent key to the genera, and to many of the species. No doubt these keys were difficult to prepare, but their usefulness, in a paper to be used by non-specialists dealing with many species of diverse genera, certainly justifies the effort. As a further aid to the non-specialist, the author has included a glossary of morphological terms used in the paper.

With each genus, Cooke includes a synonymy of the more important citations, a brief description of the type species, and the name of its designator. This latter item is of particular value because Mortensen was mistaken in his citation of many of the type species and seldom indicated the designator. Each species has a full synonymy and brief description, with comments on occurrence, age, and location of type specimens. The bibliography includes not only all the cited references, but also the titles of general works on the Cenozoic of the Americas.

The plates are excellent. Almost all species are figured, many with four views of one specimen, or several views of different specimens of a species. The profusion and high quality of the photographs make the plates one of the outstanding features of this paper. Cooke is to be congratulated on being able to place so many pictures on one plate, and at the same time on keeping the figures of one species in close proximity to each other. Furthermore, he has indicated the magnifications, when not natural size, on the plate near each figure. This procedure is most helpful and saves the reader from having to take time to check the plate explanation for each figure. It also prevents a reader from assuming that a picture is natural size.

In conclusion, this work will be most useful to both the stratigraphic paleontologist and the echinoid specialist. Because of its excellent plates, glossary, and key, the stratigraphic paleontologist should be able to identify most of the known species of Cenozoic echinoids of eastern United States that he encounters in his work. To the echinoid specialist, this paper will serve as a foundation for more detailed studies in the morphology, variation, and phylogeny of these echinoids.

PORTER M. KIER
U. S. National Museum

THE MORPHOLOGY AND ANATOMY OF THE AMERICAN SPECIES OF THE GENUS *Psaronius*. By Jeanne Morgan. Illinois Biological Monographs, No. 27. December 21, 1959. Paperbound, $3.00; clothbound, $4.00.

This monograph is a valuable contribution to our knowledge of a genus of complex Pennsylvanian and Permian tree ferns that have never become well understood. Six valid species, three new, are dealt with, and these constitute the species presently

known from North and South America. In addition, three earlier described species are relegated to synonymy, and three more names are discarded as having not been founded on adequately preserved material.

Most of the new material described was preserved in coal balls from the Upper McLeansboro group near Berryville, Illinois, and from the Cherokee shale of the Des Moines series near West Mineral, Kansas.

The relatively slender *Psaronius* stem attained a height of at least 10 m. and bore a crown of frondlike leaves at the top. Along most of the length of the stem adventitious roots emerged which as they trailed down the stem formed a thick mantle or sheath that became thicker toward the base. This root sheath thus was responsible for most of the mechanical strength of the trunk. Within this root sheath the obconical stem shows marked structural differences from the base to higher levels. On the lower portions of some stems the fronds were spirally arranged with three orthostichies, but higher, where the stem is wider, the number of orthostichies increases to as many as 14 or more, and the spiral arrangement changes to a whorled condition with the fronds in alternating verticils of seven or more each. This change in phyllotactic pattern is accompanied by a corresponding increase in the number of vascular strands that show in a particular cross section at a given level. Evidence is presented to show that the number of vascular strands and leaf orthostichies at any one horizon are not sound as specific characters.

The book provides much detailed information on the six recognized *Psaronius* species in the New World and gives a better understanding of the relation between structure and stage of development within the genus in general than we have possessed before. However, the book is not, as the title might imply, a complete work. Only one specimen is described of the well known beautifully silicified *Psaronius* trunks that occur in southern Ohio. This lone specimen rates a rather cursory description of less than one page and two figures. The quite long and rather detailed descriptions of the other five species would be considerably enhanced and rendered much easier to follow if the twenty-two line drawings assembled into plates at the back were interspersed through the text at appropriate places.

C. A. Arnold
University of Michigan

Miocene Floras of the Columbia Plateau. Part I. Chaney, Ralph W. Composition and Interpretation. Part II. Chaney, Ralph W., and Daniel I. Axelrod. Systematic Considerations. Carnegie Institution of Washington, Publication 617. viii+237 p. Illus. 1959. Paper $4.25, cloth $4.75.

Paleobotanical studies relating to the Miocene floras of western North America began as early as 1865. Studies by subsequent investigators have contributed additional information, and with the development of new techniques (i.e., pollen analysis), larger collections, and a greater knowledge of the structure, composition, distribution and ecology of modern floras, an extensive amount of information is available concerning fossil floras of the Columbia Plateau region. In this publication Chaney and Axelrod summarize existing information, supplement this data with results from their own research and present revised interpretations of the history and paleoecological significance of these Miocene floras.

Part I. Composition and Interpretation. There are twenty-two floras of Middle to Late Tertiary age in western North America. Three of these, in Oregon, are considered in detail: The Mascall flora, exposed along the East Fork of the John Day River; the Blue Mountain flora, exposed in three localities in the drainage basin of the Middle Fork of the John Day River in Grant County; and the Stinking Water flora, exposed within the Stinking Water Basin in northeastern Harney County. All are apparently of Middle Upper Miocene age.

Each of the floras is discussed under the headings, Introduction, in which previous collectors and collection sites are given; Geologic Occurrence; Composition; and Paleoecology. The Mascall formation consists of a series of rhyolite tuffs, with diatomite in the lower portions, and associated sand and gravels. Its floral composition does not correspond exactly to any modern

forest, although it is considered, with several other similar floras, to constitute the more inclusive Arcto-Tertiary Geoflora. The Mascall flora consists of megafossils from 28 families, 46 genera, and 68 species. Ten new species are described. The most abundant remains are of *Taxodium*, *Quercus*, *Carya*, *Platanus*, *Acer*, *Metasequoia*, *Ginkgo*, *Ulmus*, *Cedrela*, and *Betula* with lesser amounts of *Nyssa*, *Hydrangea*, *Typha*, *Zelkova*, *Pterocarya*, *Persea*, *Ostrya*, *Liquidambar*, *Thuja*, *Keteleeria*, *Libocedrus*, *Salix*, *Fraxinus*, *Pinus*, *Crategus*, *Abies*, *Cercidiphyllum*, *Populus*, *Fagus*, *Gymnocladus*, *Cephalotaxus*, *Sassafras*, *Smilax*, *Mahonia*, *Lindera*, *Albizzia* and others. Comparison of the fossil remains with modern floras indicates that the affinities of the Mascall flora lie with the temperate vegetation of eastern Asia, eastern North America, and western North America: "Although there is no living forest which duplicates the Mascall flora in all respects, the swamp cypress forests of the Mississippi Valley and the forests of the uplands in eastern North America and eastern Asia may together provide a basis for reconstructing the vegetation of the John Day area during the Miocene epoch."

The Blue Mountain flora is preserved in white, thin-bedded alternating layers of diatomaceous earth and volcanic sand. It consists of remains from twenty-three families, thirty-two genera, and forty-six species. Seven new species are described. There is a close species relationship between the Blue Mountain flora and the Mascall flora, but the dominant Blue Mountain species are rare in the Mascall flora. This quantitative difference is most conspicuous in the conifer element, with no dominant species in common. Chaney suggests that these differences are a reflection of topographic diversity and, as opposed to the lowland Mascall flora, "the Blue Mountain flora is made up of plants which lived on the shores of upland lakes, and on the slopes adjacent."

The Stinking Water flora is also preserved in volcanic sediments which vary from sandy shales to fine white ash with interfingering flows of basalt. Diatomite is absent. Remains from twenty-one families, twenty-six genera, and forty-one species are preserved. Seven new species are described. A close relationship exists between this flora and that of the Mascall formation. The most abundant gymnosperm, *Glyptostrobus oregonensis* Brown, is not present in the Mascall flora, but it is considered to be a lowland species. With regards to climatic affinities, Chaney states, "With the exception of *Cedrela*, *Glyptostrobus* and *Keteleeria*, all the Stinking Water genera are typically north temperate in distribution today."

A comparison is made with other Miocene floras of adjacent areas: The Latah flora of Washington and Idaho, the Payette flora of Idaho, the Succor Creek flora of Idaho and Oregon, the Trout Creek flora of Oregon, and the Upper Cedarville flora of California and Nevada. A complete and revised species list is given for each flora. It is concluded that all are of Middle Upper Miocene age and constituted four major forest types during that time: the swamp cypress forest (Mascall and Latah), the Glyptostrobus forest (Stinking Water), the evergreen oak-Gordonia-Maple forest (Blue Mountain, Payette, and Trout Creek) and the mountain conifer forest.

The last section, Correlation and Age, presents geologic and paleobotanical evidence for assuming these floras to be of the same age.

Part II. Systematic Considerations. This section represents a valuable compilation of fossil plants and pertinent literature concerned with floras of Miocene age in western North America. Under each family the genera and species are listed with references to the original descriptions, other occurrences are cited, and a brief discussion of the paleoecologic significance of the remains is presented. Twenty-four new species from the Mascall, Blue Mountain, and Stinking Water floras are described and numerous recombinations are made. The forty-four plates containing 343 illustrations and the bibliography of 191 references should contribute to make this significant publication indispensable for further investigations of Miocene floras.

ALAN GRAHAM
University of Michigan

NOTICES

PLASTER CASTS OF TEXAS CRETACEOUS TYPE INVERTEBRATES

The Bureau of Economic Geology of The University of Texas announces availability for sale or exchange of a large number of plaster casts of Texas Cretaceous type pelecypods, gastropods, ammonites, and echinoids. Represented are 87 species and 90 types, including 70 primary types (holotypes, paratypes, and syntypes), and 20 hypotypes.

More than half of the specimens are ammonites; there are also casts of type specimens of many species described by Adkins, Böse, and Cragin. Most of the original specimens have been figured in Bureau publications, and all are in the invertebrate fossil collections at the Bureau museum building on the Little Campus, 18th and Red River Streets, Austin.

A list of these available casts will be sent upon request addressed to Bureau of Economic Geology, University Station, Box 8022, Austin 12, Texas.

JOHN T. LONSDALE, Director

A TRANSFER OF TYPES AND FIGURED SPECIMENS

This communication is for the purpose of announcing the transfer of types and figured specimens from the University of Wisconsin paleontological collections to the U. S. National Museum. The bulk of this material consists of the R. P. Whitfield Collections described by Whitfield in Part 3 of Volume 4 "Geology of Wisconsin, a survey of 1873–1879" and which was published in 1882. Most of the material is Cambrian and Ordovician in age.

The purpose of the transfer is to make the collection more accessible to more students and to insure the safety and care of these important types.

ROGER L. BATTEN

SOCIETY RECORDS AND ACTIVITIES

In accordance with Article 3, Chapter 1, of the By-Laws of the Paleontological Society, the names of new members approved by the Council are as follows:

BANKS, HARLAN P., Botany Dept., Cornell University, Ithaca, N. Y.: John W. Wells, W. Storrs Cole.

BERG, LARRY DALE, 210 N. 8th Street, Grand Forks, N.D.: F. D. Holland, Jr., James Chmelik

CARLSON, CLARENCE G., University Station, Grand Forks, N.D.: F. D. Holland, Jr., James Chmelik

CARSON, CARLTON MANN, 455 East Main Street, Ventura, Calif.: Orville Lee Bandy, C. C. Church

CHAPMAN, JOHN SHERMAN, 2005 Austin, Apt. 6, Amarillo, Texas: William McBee, Jr., Paul W. Nygreen

DAVIS, LYNN (Miss), 135 Scott Hall, Oxford, Ohio: Karl E. Limper, K. E. Caster

FOSTER, NEAL ROBERT, Dept. of Conservation, Fernow Hall, Cornell University, Ithaca, N. Y. John W. Wells, W. Storrs Cole

HUGHES, RICHARD DAVID, Memorial Univ. of St. John's, Newfoundland, Canada: V. J. Okulitch, M. Y. Williams

KLUCKING, EDWARD PAUL, 1290 Hopkins Street, Apt. 5, Berkeley 2, California: Wayne L. Fry, R. L. Langenheim, Jr.

LEEDS, HARRIET DEE, 211 Scott Hall, Miami University, Oxford, Ohio: Karl E. Limper, Kenneth E. Caster

NORFORD, BRIAN SEELEY, Shell Oil Co. of Canada, Box 100, Calgary, Alberta, Canada: Carl O. Dunbar, Karl M. Waagé

OSGOOD, RICHARD GROSVENOR, JR., Dept. of Geology, Univ. of Cincinnati, Ohio: K. E. Caster, John N. Pope

PHILLIPS, TOMMY LEE, Henry Shaw School of Botany, Washington University, St. Louis 5, Missouri: James M. Schopf, Henry N. Andrew, Jr.

RAYMOND, WILLIAM HENRY II, 22 East Walnut Street, Oxford, Ohio: K. E. Caster, Karl E. Limper

REINHART, ROY HERBERT, Dept. of Geology, Miami University, Oxford, Ohio: K. E. Caster, John N. Pope

RODRIGUEZ, JOAQUIN, Dept. of Geology and Geography, Hunter College, Bedford Park, Boulevard West, New York 68, N. Y.: R. M. Finks, Frederick P. Young

ROELLIG, HAROLD FREDERICK, 310 W. 105th Street, New York 25, N. Y.: Edwin H. Colbert, Norman D. Newell

ROWELL, ALBERT JOHN, Department of Geology, Nottingham University, Nottingham, England: Richard Cifelli, G. Arthur Cooper

SINGH, YOGENDRA LALL, Nepal Bureau of Mines, Kathmandu, Nepal: Stuart A. Northrup, Sidney R. Ash

SOCIETY NEWS

The Council of the Paleontological Society has established an Endowment Fund for the Society, the proceeds from which will be devoted to the publication requirements of the Society. It is heartening to acknowledge the first contribution to this fund by the Paleontological Society of Washington (D. C.) in the amount of fifty dollars.

In his letter accompanying the check from the Paleontological Society of Washington, President Norman F. Sohl wrote as follows:

"We hope that this contribution will initiate establishment of a permanent fund in the Paleontological Society, and encourage other groups and individuals who are concerned for the future of the *Journal of Paleontology* to support it beyond mere payment of dues."

To these generous and hopeful words I would like to add my own AMEN and that of the Council of the Paleontological Society!

KENNETH E. CASTER, President,
Paleontological Society

SPECIAL PROGRAM ON TECHNIQUES

The Paleontological Society will have as part of its program at the Denver meeting of the Geological Society of America in November a special session devoted to paleontological techniques. This special program is to consist mainly of demonstrations of fossils and the materials and techniques used for their study. We hope to have a large meeting room lined by small tables where each participant will be able to display his "wares." In this fashion the meeting will provide a medium for informal discussions.

A short session of formally presented papers is also planned especially for those with contributions not readily handled by the demonstration technique. Anyone who wishes to participate in this program is encouraged to write to Bernhard Kummel, Museum of Comparative Zoology, Harvard University, Cambridge, Mass.

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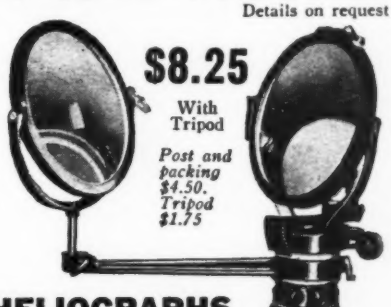

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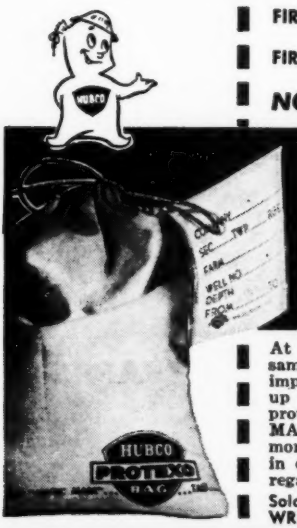

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